Ernst Mayr Library, MCZ
MCZ 125A

WIL
8424
.6

HARVARD UNIVERSITY

Ernst Mayr Library
of the Museum of
Comparative Zoology

MCZ
LIBRARY
JAN 18 2011
HARVARD
UNIVERSITY

84 24
b

The Wilson Journal *of Ornithology*

Volume 120, Number 1, March 2008

MCZ
LIBRARY
MAY 19 2009
HARVARD
UNIVERSITY

Published by the
Wilson Ornithological Society

THE WILSON ORNITHOLOGICAL SOCIETY
FOUNDED 3 DECEMBER 1888
Named after ALEXANDER WILSON, the first American ornithologist.

President—James D. Rising, Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada; e-mail: rising@zoo.utoronto.ca

First Vice-President—E. Dale Kennedy, Biology Department, Albion College, Albion, MI 49224, USA; e-mail: dkennedy@albion.edu

Second Vice-President—Robert C. Beason, USDA, Wildlife Services, 6100 Columbus Ave, Sandusky, OH 44870, USA; e-mail: beason@netzero.com

Editor—Clait E. Braun, 5572 North Ventana Vista Road, Tucson, AZ 85750, USA; e-mail: TWILSONJO@comcast.net

Secretary—John A. Smallwood, Department of Biology and Molecular Biology, Montclair State University, Montclair, NJ 07043, USA; e-mail: smallwoodj@montclair.edu

Treasurer—Melinda M. Clark, 52684 Highland Drive, South Bend, IN 46635, USA; e-mail: MClark@tcservices.biz

Elected Council Members—Robert L. Curry; Daniel Klem Jr., and Douglas W. White (terms expire 2008); Carla J. Dove, Greg H. Farley, and Mia R. Revels (terms expire 2009); Rebecca Holberton, Robert S. Mulvihill, and Timothy O'Connell (terms expire 2010).

Membership dues per calendar year are: Active, $21.00; Student, $15.00; Family, $25.00; Sustaining, $30.00; Life memberships, $500 (payable in four installments).

The Wilson Journal of Ornithology is sent to all members not in arrears for dues.

THE WILSON JOURNAL OF ORNITHOLOGY
(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

All articles and communications for publications should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109.

Subscriptions, changes of address, and claims for undelivered copies should be sent to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710. Phone: (254) 399-9636; e-mail: business@osnabirds.org. Back issues or single copies are available for $12.00 each. Most back issues of the journal are available and may be ordered from OSNA. Special prices will be quoted for quantity orders. All issues of the journal published before 2000 are accessible on a free Web site at the University of New Mexico library (http://elibrary.unm.edu/sora/). The site is fully searchable, and full-text reproductions of all papers (including illustrations) are available as either PDF or DjVu files.

© Copyright 2008 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

COVER: Wilson's Snipe (*Gallinago delicata*). Illustration by Scott Rashid.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

MCZ
LIBRARY
MAY 19 2009
HARVARD
UNIVERSITY

FRONTISPIECE. *Zosterops somadikartai,* sp. nov., Togian White-eye, a new species of white-eye endemic to mangroves and lowland secondary woodlands in the Togian Islands, Sulawesi, Indonesia. Adult male (holotype); original painting by Agus Prijono.

The Wilson Journal *of Ornithology*

Published by the Wilson Ornithological Society

VOL. 120, NO. 1 March 2008 PAGES 1–238

The Wilson Journal of Ornithology 120(1):1–9, 2008

A NEW WHITE-EYE (*ZOSTEROPS*) FROM THE TOGIAN ISLANDS, SULAWESI, INDONESIA

MOCHAMAD INDRAWAN,[1] PAMELA C. RASMUSSEN,[2,4] AND SUNARTO[1,3]

ABSTRACT.—We encountered white-eyes (*Zosterops*) that did not match any known species during ornithological field observations in the Togian Islands, Gulf of Tomini, Sulawesi, Indonesia. Subsequently, we collected a specimen and made tape recordings. We consider the *Zosterops* of the Togian Islands to be a new species that differs most strikingly from the Black-crowned White-eye (*Z. atrifrons*) in lacking a white eye ring and in soft-part colors. The new species has a somewhat higher-pitched, less modulated song than *Z. atrifrons*. It seems uncommon and has been encountered only near sea level on three small islands, and it may be best considered Endangered. This brings the number of endemic species in the Togian Islands to two and, under BirdLife International criteria, this island group (which has recently been declared a National Park) now qualifies as an Endemic Bird Area. *Received 17 April 2006. Accepted 25 May 2007.*

The white-eyes (*Zosterops*) of Indonesia comprise a bewildering and diverse array of taxa. No fewer than 10 taxa in six species (Everett's White-eye [*Z. everetti*], Mountain White-eye [*Z. montanus*], Lemon-bellied White-eye [*Z. chloris*], Pale-bellied White-eye [*Z. consobrinorum*], Lemon-throated White-eye [*Z. anomalus*], and Black-crowned White-eye [*Z. atrifrons*]; Mees 1961, White and Bruce 1986) have been conventionally recognized from the Sulawesi subregion alone. Despite this, it recently has become clear that Mees' (1961) classification substantially underestimates the diversity of *Zosterops* taxa of the Sulawesi subregion. Taxa formerly considered subspecies of *Z. atrifrons* that are clearly better considered full biological species include the Sangihe White-eye (*Z. nehrkorni*) and the extralimital Seram White-eye (*Z. stalkeri*) (Rasmussen et al. 2000, Dickinson 2003). Formerly synonymized subspecies of *Z. atrifrons* requiring recognition include *Z. a. subatrifrons* and *Z. a. surdus* (Rasmussen et al. 2000) and a probably undescribed form of *Z. atrifrons* occurs in south-central Sulawesi (Holmes and Holmes 1985). Most surprisingly, at least two distinctive new taxa have re-

[1] Department of Biology, Faculty of Science and Mathematics, University of Indonesia, Depok Campus, Depok 16424, Indonesia.

[2] Michigan State University Department of Zoology and Museum, West Circle Drive, East Lansing, MI 48824, USA.

[3] Department of Fisheries and Wildlife Science, College of Natural Resources, 210 Cheatham Hall, Virginia Tech University, VA 24060, USA.

[4] Corresponding author;
e-mail: rasmus39@msu.edu

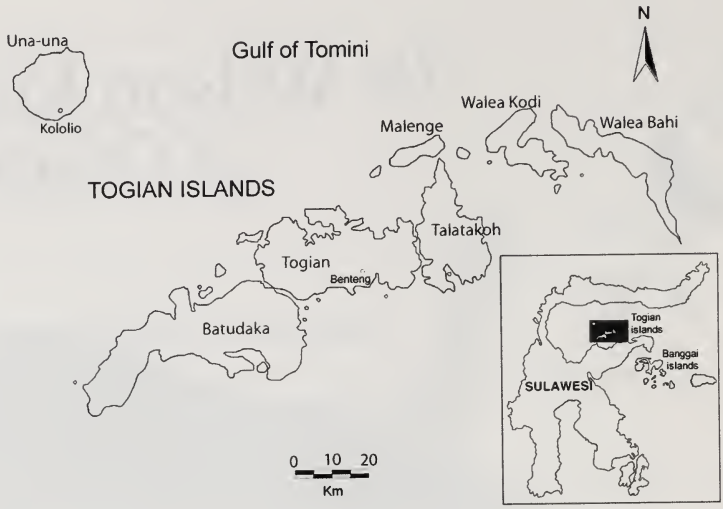


FIG. 1. Relevant localities in the Togian Islands, eastern Sulawesi, and the Banggai Islands.

cently been discovered; one, a member of the *Z. consobrinorum* group from Wangi Wangi in the Tukangbesi Islands (off Sulawesi's southeast peninsula) is still formally undescribed (Owen 2004; David Kelly, pers. comm.), while the other is the subject of this paper. We now know there are at least 15 taxa and 9–10 full biological species of *Zosterops* in the Sulawesi subregion. Few of these forms overlap in geographic range and several are restricted to one or two peninsular "arms" of Sulawesi or one or a few of its satellite islands. Even more taxa of *Zosterops* may await discovery in this highly complex and poorly surveyed region, not only in remote islands, but also in the less explored mountain ranges of Sulawesi's several peninsulas.

The first documented ornithological work in the Togian Islands (now also spelled Togean Islands), Gulf of Tomini, Sulawesi, Indonesia (Fig. 1) was in August 1871 by A. B. Meyer (Indrawan et al. 2006). The only other bird collector to have worked there was J. J. Menden in the fall of 1939 (Indrawan et al. 2006). Subsequent ornithological work in the Togian Islands has been of limited duration and strictly observational. However, longer-term field observations in the Togian Islands (1–28 Aug 1996, 3–27 Jun 1997, and 11–18 May 2001) and Bangkurung Island (Banggai Archipelago, 2–8 Nov 1997) resulted in discovery of a new species of owl (Indrawan and Somadikarta 2004) and observations of white-eyes (Frontispiece) in the field (by MI and Sunarto). White-eyes on the Togian Islands (but not those of Bangkurung) are similar in most characters to the Black-crowned White-eye (*Z. atrifrons*) of Sulawesi, except they entirely lack the white eye ring, which is prominent in adults of all forms of *Z. atrifrons* (Rasmussen et al. 2000, Dickinson 2003), and narrower but still conspicuous in juveniles (Rasmussen et al. 2000).

We observed *Z. atrifrons* in the eastern and northern peninsulas of Sulawesi to compare with our sightings in the Togian Islands. The observations in the eastern peninsula were in Tanjung Api Nature Reserve (16–19 and 24–27 Jan 2003), while those in the northern peninsula were in Tomohon (4–5 Jan 2002, 31 Jul 2003) and Tangkoko Nature Reserve (30 Jul 2003) (MI, unpubl. data).

MI revisited the Togian Islands in July 2003 and collected a single specimen (Frontispiece). This is the first museum specimen of *Zosterops* known from either the Togian Islands or Bangkurung Island. The Togian Islands specimen was directly compared by PCR at AMNH (acronyms in Acknowledgments) with 29 *Z. a. atrifrons*, two *Z. atrifrons* (race uncertain) from Siuna (00° 45′ S, 122° 58′ E), east-central Sulawesi, three *Z. a. surdus* from west-central Sulawesi, five *Z. a. sulaensis* from the Sula Islands, and four *Z. a. subatrifrons* from Peleng Island, Banggai Islands; at BMNH with six nominate *atrifrons*

and three *Z. anomalus*; at USNM with series of nominate *atrifrons* and *surdus*; and indirectly using photographs at RMNH with two *anomalus*, four nominate *atrifrons*, four *sulaensis*, and five *Z. stalkeri*.

We compared songs and calls of the white-eye from the Togian Islands with those of *Z. a. atrifrons* and *surdus* ($n = 4$), *Z. a. sulaensis* (1), *Z. nehrkorni* (1), *Z. h. hypoxanthus* of New Britain (2), and *Z. h. admiralitatis* of Manus (1); recordings of vocalizations of other taxa were unavailable to us. The new white-eye differs strikingly in plumage from other known taxa, being closest to *Z. a. atrifrons*, and it appears to differ consistently in song from *Z. atrifrons*. Given that the magnitude of the several differences exceeds those between most other currently recognized species of *Zosterops*, and that lack of an eye ring, iris color, and song differences could well serve as isolating mechanisms, the new taxon should be considered specifically distinct under the Biological Species Concept. We propose for it the name:

Zosterops somadikartai, sp. nov.
Togian White-eye

Holotype.—Museum Zoologicum Bogoriensis 30366, male, from Pulau Malenge (00° 15′ S, 122° 03′ E, ~50 m asl), Togian Islands, Gulf of Tomini, Sulawesi, collected 27 July 2003 by MI. Specimen in heavy molt of wing and body, and has lost feathers from right side of venter, lower undertail coverts, all uppertail coverts, and entire tail. Detached feathers saved at time of collection include one right and four left rectrices, one belly feather, two ventral flank feathers and three from more dorsally on the flanks, and five uppertail coverts. Holotype an adult based on compact feather structure, especially on nape and mantle; broad-tipped outer remiges in comparison with two known juvenile *surdus*; heavy molt; flaking tarsal scutes, and (as shown by a radiograph) evidently fully ossified cranium.

Diagnosis.—*Zosterops somadikartai* differs from nominate *atrifrons* (of northern Sulawesi) in its slightly less extensive black cap, which does not reach the upper rear eye and which appears to have a straight rather than oblique border at the rear edge; in its lack of a white eye ring (vs. a medium-width white eye ring); its clearer yellow throat, less invaded by olive on the sides and the yellow not extending onto the upper breast; its whiter underparts; its slightly heavier bill than most *atrifrons*, with a distinctly pale base; and its reddish (vs. brown) iris. Measurements of the holotype suggest slightly different proportions from *atrifrons* (Table 1) but cannot be taken as definitive given that only a single individual of *somadikartai* was available for measurement. From *surdus* (of west-central Sulawesi), *somadikartai* differs in the same ways as from *atrifrons*, but is paler and brighter olive above and much clearer yellow on the throat. *Zosterops somadikartai* differs from *subatrifrons* (of Peleng Island, Banggai Islands) by its lack of a white eye ring (vs. a fairly broad white eye ring); its grayer breast, and its less extensive black crown. From *sulaensis* (of the Sula Islands), *somadikartai* differs by its lack of a white eye ring (vs. a very broad white eye ring); by its slightly narrower-based bill; its less extensive black crown; its grayish (vs. white) breast; and its duller yellow-olive upperparts. From *Z. m. minor* (of western New Guinea, which also lacks a white eye ring but which also has tiny white specks around the orbital skin), *somadikartai* differs in having a narrower-based bill; blacker (vs. grayish) bare skin around the eye; in having a black forecrown (vs. forecrown olive, essentially concolorous with mantle); in being much duller olive above; in having a gray (vs. white) breast; and in having a much duller, less orange throat. From *Z. anomalus* (of southern Sulawesi, which lacks a white eye ring but also has tiny white specks around the orbital skin), *somadikartai* differs in its smaller size; distinctly thinner bill (on dorsal view); black (vs. bright yellow-olive) forecrown and lores (vs. yellow); duller olive upperparts; less extensive, less bright yellow throat; blacker (vs. dark brown) wingtips; and whiter central underparts (*anomalus* is incorrectly shown as having a white vent in Coates and Bishop [1997]; it actually has a yellow vent as with *somadikartai*). No other regional taxa of *Zosterops* are as similar to *somadikartai* as those listed above.

Description of the Holotype.—Capitalized color and number descriptions follow Smithe (1975). Forehead from base of bill to above eye Jet Black (89); bare orbital ring blackish-gray with tiny white specks (latter visible only

at close range), surrounded by Jet Black feathered eye ring; rear crown and nape Citrine (51), grading on auriculars to Yellowish Olive-Green (50), and on lower sides of face to Olive-Yellow (52), then to Sulfur Yellow (157) at center of throat. Back Citrine, rump Yellowish Olive-Green. Wing coverts Olive-Green (Basic [46]), marginal coverts paler than Sulfur Yellow, alula Blackish Neutral Gray (82), primary and secondary edgings Yellowish Olive-Green, tips of primaries and secondaries between Blackish Neutral Gray and Jet Black, tertials Citrine, underwing coverts whitish. Upper tail coverts and rectrices detached and central rectrices missing and color cannot reliably be described. Rectrices dark brownish-black with weakly olive lateral edgings (as in many *atrifrons* and *surdus*) when arranged as in folded tail. Undertail coverts missing. Upper breast paler than Pale Neutral Gray (86), lower breast to belly and flanks white, tibial feathers white on internal side, grayer externally, vent Sulfur Yellow. Iris dark red (from photographs taken of holotype while living). In life, the basal third of the lower mandible was pale flesh, although when dried the bill of the same individual appears completely black except for the rami of the lower mandible, which are a dull pinkish horn. The bare fleshy eye ring was dark grayish in life, but is blackish in the specimen. The feet are fairly pale in the photograph in which they are visible, but are dark metallic horn in the specimen.

Measurements of the Holotype.—Measurements (mm) were taken by PCR. Head and body length of dried specimen (forecrown at base of bill to vent) ~65; culmen (from feathering) 11.0; wing arc 57; tail missing, but longest feather (from tip to proximal end of pigmentation on dorsal shaft) 40.2; tarsus 14.9 (Table 1).

Etymology.—We are pleased to name this new species after Professor Soekarja Somadikarta, Indonesia's leading avian taxonomist. Dr. Somadikarta encouraged the senior author to work on taxonomic aspects of birds of Sulawesi (resulting in the discovery of two new bird species), and for many years contributed significantly to Indonesian ornithology, especially in taxonomy.

Specimens.—The holotype is the only known specimen of *Z. somadikartai*.

REMARKS

Voice

Song.—The song of *Z. somadikartai* is a thin sweet warble, fairly similar overall to that of *Z. atrifrons* (Fig. 2), which is somewhat variable among available recordings. Successive song strophes of what is evidently the same individual of *atrifrons* are typically similar to one another. Five successive song strophes for *somadikartai*, probably from the same individual, are available and, despite the complexity of the song, all these strophes are extremely similar, differing at most by the dropping of a single note near the end of the strophe. The song sample of *somadikartai* differs consistently from that of *atrifrons* in sounding distinctly higher overall. There is broad overlap of frequencies between the two taxa, but the frequency range of *atrifrons* is broader (4.2 to 7.3 kHz for *somadikartai* vs. 3.0 to 7.7 kHz for *atrifrons*). The song of *somadikartai* also differs from *atrifrons* in being notably less modulated, with nearly all elements having a much narrower frequency range (maximum modulation per element 0.4 kHz for *somadikartai* vs. 2.4 kHz for *atrifrons*). Two of the three available song samples of *atrifrons* end with a faint 2- to 4-note "trill" of short chip notes and, although this appears to be lacking in the third sample, it may possibly have been too faint to appear in this poor-quality recording. None of the available song strophes of *somadikartai* has trills at the end or elsewhere in the song.

The song of *somadikartai* is much higher-pitched overall (frequency range 2.1 to 5.2 kHz in *sulaensis*) compared to *Z. a. sulaensis* (Fig. 2), considered in Rasmussen et al. (2000) to probably be a good species pending further study. The song of *sulaensis* has less frequency modulation than *atrifrons*, but more than *somadikartai*.

Calls.—MI tape-recorded numerous call notes in the presence of *Z. somadikartai*, but none resemble known call notes of *Z. a. sulaensis* and no tapes were available for call notes of *Z. a. atrifrons* or *Z. a. surdus* for comparison. Small flocks of *somadikartai* gave twittering chirrups, evidently similar to those described by Watling (1983) for *Z. a. surdus*. The calls, uttered while the birds were moving, aided in their detection.

TABLE 1. Measurements ($\bar{x}$ ± SD (n)) of *Z. somadikartai*, Wallacean *Z. atrifrons* taxa, *Z. nehrkorni*, and *Z. anomalus*. Measurements of taxa other than *somadikartai* and *anomalus* are from Rasmussen et al. (2000). Primary shortfalls are distances from tip of each primary to wingtip of folded wing.

Variable	Taxon						
	somadikartai	*atrifrons*	*surdus*	*subatrifrons*	*sulaensis*	*nehrkorni*	*anomalus*
Culmen length from skull	13.8	13.3 ± 0.6 (34)	14.4 ± 0.7 (14)	14.2 ± 0.3 (5)	14.8 ± 0.6 (9)	15.9	15.3 ± 0.6 (5)
Bill width at nares	2.6	2.9 ± 0.3 (34)	2.9 ± 0.2 (14)	3.0 ± 0.2 (5)	3.0 ± 0.3 (10)	3.3	3.2 ± 0.1 (5)
Extent of black crown (adults)	7.0	10.6 ± 1.5 (31)	11.0 ± 1.6 (13)	15.3 ± 0.1 (2)	17.0 ± 1.4 (8)	9.1	
Wing length (flattened)	57	53.3 ± 1.2 (35)	57.1 ± 2.2 (14)	54.7 ± 2.4 (5)	56.6 ± 1.5 (10)	59.0	55.9 ± 2.1 (5)
P1 shortfall	6.3	5.6 ± 0.8 (29)	6.1 ± 1.1 (12)	6.0 ± 0.7 (4)	6.3 ± 0.9 (9)	6.9	5.7 ± 1.1 (3)
P2 shortfall	1.8	1.7 ± 0.6 (28)	1.9 ± 0.7 (12)	1.7 ± 0.2 (4)	1.9 ± 0.5 (9)	3.3	1.5 ± 0.5 (3)
P3 shortfall	0	0.2 ± 0.3 (27)	0.4 ± 0.6 (12)	0.4 ± 0.5 (4)	0.2 ± 0.6 (9)	1.4	0.7 ± 0.3 (3)
P4 shortfall	0	0.1 ± 0.3 (26)	0.1 ± 0.4 (12)	0.1 ± 0.2 (4)	0.0 ± 0 (9)	0.0	0.0 ± 0 (3)
Tarsus length	14.9	16.0 ± 1.1 (34)	17.7 ± 1.4 (14)	16.7 ± 0.9 (4)	16.4 ± 0.5 (8)	17.0	16.6 ± 0.6 (5)
Tarsus distal width	2.4	2.3 ± 0.2 (35)	2.4 ± 0.1 (14)	2.4 ± 0.0 (5)	2.5 ± 0.1 (10)	3.0	2.6 ± 0.2 (5)
Midclaw length	4.1	4.0 ± 0.4 (35)	4.2 ± 0.4 (14)	4.1 ± 0.5 (5)	4.3 ± 0.3 (8)	4.4	4.4 ± 0.2 (5)
Hallux claw length	5.6	5.1 ± 0.2 (34)	5.6 ± 0.2 (13)	4.8 ± 0.3 (4)	5.0 ± 0.4 (6)	5.8	5.6 ± 0.2 (5)
Hallux length	5.8	4.7 ± 0.4 (29)	5.1 ± 0.4 (12)	5.1 ± 0.3 (4)	5.1 ± 0.7 (9)	5.3	5.7 ± 0.4 (5)
Tail length	40.2[a]	37.3 ± 1.2 (35)	40.3 ± 1.5 (35)	38.0 ± 2.7 (4)	39.7 ± 1.7 (10)	40.5	44.0 (1)

[a] Length of longest detached feather to proximal end of pigmentation on dorsal side of calamus.

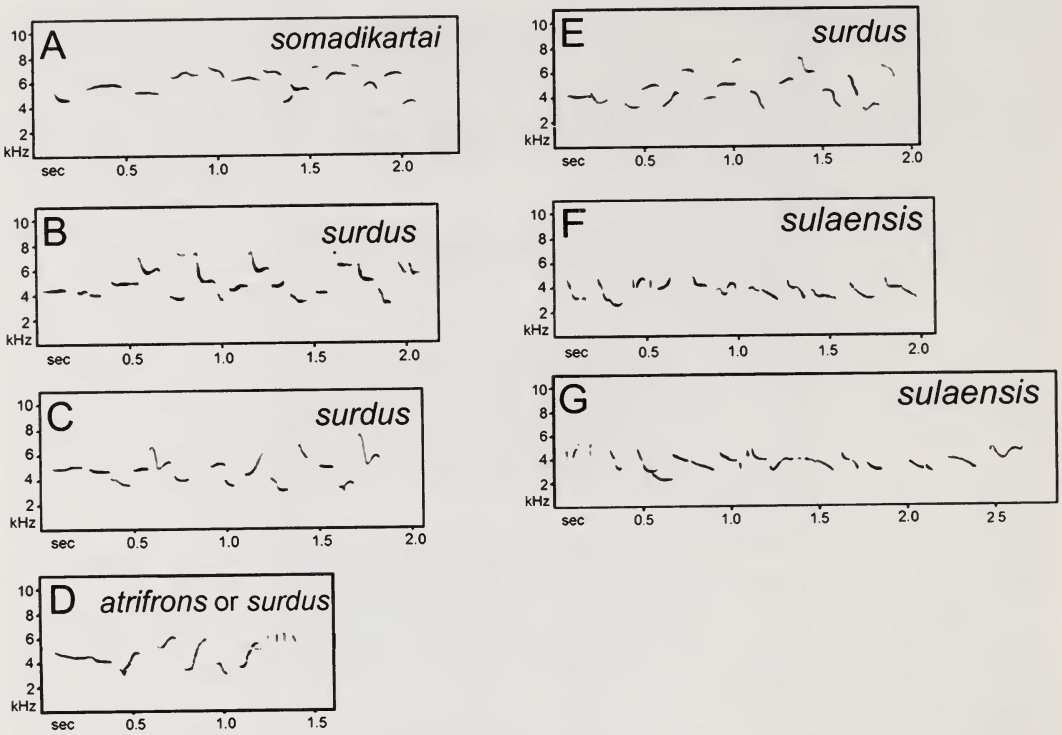


FIG. 2. Sonagrams of (A) *Z. somadikartai*, recording by MI; (B) *Z. atrifrons surdus*, NSA 32916, Lore Lindu, Sulawesi, recording by Alan Greensmith; (C) *Z. atrifrons surdus*, NSA 45860, Lore Lindu, Sulawesi, recording by Steven Smith; (D) *Z. atrifrons* (subspecies uncertain, either *surdus* or *atrifrons*), NSA 13189, Sulawesi, recording by R. J. Watling; (E) *Z. atrifrons surdus*, NSA 113121, Sulawesi, recording by Clide Carter; (F, G) two recordings of *Z. a. sulaensis*, NSA 73891, Taliabu, Sula Islands, by Robert Lucking.

Rationale for Consideration as a Full Biological Species

The alpha taxonomy of few groups of birds is as difficult and ambiguous as that of the *Zosterops* white-eyes, given the large number of mostly allopatric taxa and the small number of morphological characters that vary among taxa. Taxa from widely disparate parts of the world can appear extremely similar without necessarily indicating close relationships. Numerous similar-looking white-eye taxa that were long treated as conspecific have recently been found to have high levels of genetic divergence inconsistent with subspecies status, for example among Micronesian (Slikas et al. 2000) and African and Indian Ocean taxa (Warren et al. 2006). In at least one African case, taxa formerly united as conspecific are not even sister taxa, instead being widely separated on the phylogenetic tree (Warren et al. 2006). The former unification of many dissimilar taxa under Black-crowned White-eye (*Zosterops atrifrons*) is the only case of which we are aware in which just one "subspecies" (*minor*) of a polytypic species lacks a white eye ring, but *minor* was subsumed under *atrifrons* on the basis of a single putative hybrid specimen and is best treated as a separate species (Rasmussen et al. 2000). In the case of *Z. somadikartai*, it might be argued that it is just a strongly marked subspecies, but we consider that its level of distinctiveness is equivalent to that of Black-fronted White-eye (*Z. minor*) and numerous other taxa now usually treated as full species. In our view, the lack of an eye ring, the iris and bill color differences, and the divergence in song would likely act as isolating mechanisms. Hence we choose to describe *somadikartai* at the level of full species under the Biological Species Concept.

Distribution

Zosterops somadikartai is endemic to the Togian Islands, Gulf of Tomini, Sulawesi. It

has been recorded from several sites on Malenge Island (00° 15′ S, 122° 03′ E), Binuang, Talatakoh Island (00° 21′ S, 122° 06′ E), and two sites at Batudaka Island (00° 28′ S, 121° 48′ E). All records except for the holotype are sight records. All localities were below 100 m asl.

Several observations of the new white-eye were made by MI and Sunarto in the Togian Islands prior to the collection of the type specimen.

23 and 27 August 1996, and 21 June 1997 (Malangkat, Malenge Island).—Two, three, and two birds, respectively were observed traveling and foraging on low bushes (probably *Lantana camara*) near mangroves (*Avicennia* and *Sonneratia* spp. behind the mud-living *Rhizophora* sp. community). The observations lasted between 30 sec and 1 min each from a distance of ~20 to 40 m.

12 June 1997 (Malenge Village, Malenge Island).—Two birds were seen moving through a garden with coconuts (*Cocos nucifera*), other trees, and bushes. The observations were for about 30 sec from a distance of ~30 m.

23 and 28 June 1997 (Binuang, Talatakoh Island, 00°21′S, 122°06′E).—Three and two birds, respectively, were seen foraging in regenerating scrub at a logged-over forest site. Each group was observed for about 2 min each at a distance of ~10 and 20 m.

24 May 2001 (Tanempo, Batudaka Island, 00°28′S, 121°48′E).—One white-eye was briefly detected as it gleaned on exposed *Lantana* branches at 2-m height for ~5 sec, before being chased into the scrub by another white-eye. It perched and gleaned at a distance of ~15 to 20 m from us for about 3 sec. In this fleeting glimpse the bird appeared to have a narrow streak of white above the eye, although it clearly did not form an eye ring. This observation on Batudaka might differ from the others and confirmation is needed.

22 January 2003 (Bomba, Batudaka Island).—A possible additional record on Batudaka was made by Yunus Masala. Two white-eyes were observed calling and mating in a coconut grove on 22 January 2003. The birds were identified as *Zosterops anomalus*, based on their lack of a white eye ring (Y. Masala, pers. comm.). However, given the locality they were almost certainly *Z. somadikartai*.

In each of the above sightings by MI and Sunarto, the birds had a black mask covering the eye and cheek, not reaching the back of head or crown. They lacked a distinct white eye ring. The upperparts were olive and the tail dark. The throat was bright yellow, contrasting with the pale breast and underparts. The vent was yellow like the throat and contrasted with the rest of the underparts. The extent of yellow on the vent was moderate. The bill appeared black and the feet were grayish. These characters would have identified the birds as *Z. atrifrons*, except that no white eye ring was visible in all the birds observed, even from close range. The observations were of at least nine birds from four different localities on three islands within the Togian Islands.

Observations of White-eyes in the Banggai Islands.—MI made four sightings of at least three different white-eyes in the scrubby gardens of Kalopapi (Bangkurung or Bangkulu Island, 01° 50′ S, 123° 06′ E; BAKOSURTANAL [1993]) in the Banggai Islands. In these observations, the eye ring was strikingly large, resembling that of *Z. a. sulaensis*. This contrasted to MI's earlier observations (Indrawan et al. 1997) of at least eight individual white-eyes in Peleng and Banggai (Banggai Island group, which is closer to the Sulawesi mainland) in which the eye ring appeared less extensive, resembling *Z. a. atrifrons* and *Z. a. surdus* of mainland Sulawesi. The four AMNH specimens from Peleng, Banggai Islands (race *Z. a. subatrifrons*) are somewhat variable in eye ring size but are intermediate between *sulaensis* and *atrifrons*. Birds apparently with large eye rings were also observed on Banggai Island itself in 1981, but were identified as *Zosterops* cf. *chloris* (Bishop 1992). It may well be that a distinct form occurs on the outlying island of Bangkurung, or this population may be indistinguishable from *sulaensis*, but further observations and probably specimen collection will be necessary. The white-eye observations for Bangkurung were mostly in the hills, above 100 m, where the bird appeared to be moderately common in small flocks, in contrast to *somadikartai* of the Togian Islands.

Observations of White-eyes in the Eastern Peninsula of Sulawesi.—It is not clear from

the literature (e.g., White and Bruce 1986) whether any form of *atrifrons* is known from the eastern peninsula of Sulawesi. However, MI observed white-eyes in mixed garden shrubs in Tanjung Api Nature Reserve (00° 50′ S, 121° 37′ E) in the eastern peninsula of Sulawesi in 2003. Four birds from different flocks that MI observed fairly well had a clear white eye ring, and other characters (black face mask, olive mantle, and dull yellow throat) identifying them as *Zosterops atrifrons*. Their bills appeared dark and their legs gray. Two AMNH specimens recently collected from Siuna (00° 45′ S, 122° 58′ E), close to the base of the Balantak Mountains near the eastern tip of east-central Sulawesi, are similar in appearance to nominate *atrifrons*.

Ecology and Behavior

The ecology of birds and habitats in the Togian Islands is described in Indrawan et al. (2006). Monsoon and evergreen forest, interspersed with mixed gardens of coconut, clove (*Syzygium aromaticum*), cacao (*Theobroma cacao*), and durian (*Durio zibethinus*) characterize the general vegetation of the island group. The habitats in which we found *Z. somadikartai* range from mangrove to secondary vegetation and mixed gardens, all in the lowlands (<100 m asl). We did not detect the species at higher altitudes in our survey.

Zosterops somadikartai is gregarious, foraging in twos and threes, and it roosts in groups of up to five birds. The birds often foraged actively throughout the day until about sunset before retiring to roost. They fed on insects, including caterpillars, frequently by gleaning them from branches and below leaves. They often foraged in dense shrubs, possibly because these microhabitats had more insects. The roosts were typically in shrubs 5 to 15 m high, such as *Macaranga* and larger bamboos, in which they perched at 4 to 10 m above ground. An observation was also made of two birds roosting in the midcanopy of mangroves at 1130 UTC+8.

Conservation Status

Our limited observations suggest that *Zosterops somadikartai* may be localized and uncommon. The bird definitely occurred in at least three of the six main islands of the Togian Islands, namely Malenge, Talatakoh, and Batudaka (Fig. 1). It has not been found on Togian and the Walea islands, although its presence on these islands could have been overlooked. That all previous collectors and observers failed to detect this species supports the conclusion from our fieldwork of its scarcity.

The present surveys allow us to suggest an IUCN threat category (IUCN 2001) for *Z. somadikartai*. The extent of occurrence of the entire population is <5,000 km^2. The population appears to be severely fragmented and the species is known to exist on just three islands. Our surveys also project that area, and extent and quality of habitat are likely to decrease further due to conversion and overexploitation of resources. We believe the taxon should be assigned "Endangered" status based on these IUCN criteria (EN, B, 1, a, b, iii). However, it does occur in some anthropogenic habitats, and further fieldwork is clearly needed to establish its population size and ecological requirements.

Endemic Bird Areas (EBAs) encompass the complete ranges of two or more restricted-range species, defined as species with an estimated total global breeding range below 50,000 km^2 (ICBP 1992, Stattersfield et al. 1998). The Togian Islands merit EBA status, given the presence there of another recently discovered endemic, Togian Hawk Owl (*Ninox burhani*) (Indrawan and Somadikarta 2004). The recently created Togean Islands National Park should afford these new bird species some of the protection necessary for their survival.

Note Added in Proof.—Zosterops somadikartai was observed in two different areas of Malenge Island on 14 and 15 December 2007, and a freshly dead individual was found just outside Malenge village (Raphael Jordan and Benoit Segerer, in litt.). This bird was not salvaged but a digital photograph shows it to be similar to the holotype. There is a large area of bare dusky circumorbital skin, bluish in front of and above the eye and below and behind the eye, with a few tiny white feathers forming barely visible white specks around the upper and lower front edges of the eye (but not on the cranial or caudal edges and not nearly forming a complete ring). Iris dark red; base of lower mandible pale pinkish horn,

contrasting with the black distal two-thirds; tarsi, toes, and claws light bluish-silver, joints slightly darker; undertail coverts pale clear yellow; and rectrices dusky black with indistinct yellowish-green edgings.

ACKNOWLEDGMENTS

This study was undertaken at the behest of Dr. Soekarja Somadikarta, who also kindly commented on the manuscript. We thank the Biology Research Center—Indonesian Institute of Sciences for research permission. We thank Dr. S. N. Prijono, Don Darjono, and Sudaryanti for sending the specimen from the Museum Zoologicum Bogoriense to the USA for study, and for their patience with the length of the loan period. Agus Prijono graciously painted the Plate of the type specimen and Yunus Masala provided data on a sighting. We thank the staff of the American Museum of Natural History (AMNH), The Natural History Museum (BMNH), Naturalis, Leiden (RMNH), the National Museum of Natural History, Smithsonian Institution (USNM), and Michigan State University Museum for access to and/or loan of specimens. Fieldwork in the eastern peninsula and offshore islands has been supported by grants, including Nagao—Natural Environment Foundation (NEF) and the Oriental Bird Club. An Earthwatch Expeditions grant (awarded to Dr. Jatna Supriatna) further augmented the funding support. We thank D. S. Rosenstein and J. G. Sikarskie for radiographs, and Cheryl Tipp and Richard Ranft for generously providing recordings of other species.

LITERATURE CITED

BAKOSURTANAL [Indonesian Surveillance and Mapping Agency, in collaboration with DISHIDROS TNI AL—Hydro-oceanographic Office of the Indonesian Navy]. 1993. Map of national marine environment Number 24. Central Sulawesi (scale 1:500,000). BAKOSURTANAL, Cibinong, Indonesia.

Bishop, K. D. 1992. New and interesting records of birds in Wallacea. Kukila 6:8–34.

Coates, B. J. and K. D. Bishop. 1997. A guide to the birds of Wallacea. Dove Publications, Alderley, Queensland, Australia.

Dickinson, E. C. (Editor). 2003. The Howard and Moore complete checklist of the birds of the world. Revised and enlarged. Third Edition. Christopher Helm, London, United Kingdom.

Holmes, P. R. and H. J. Holmes. 1985. Notes on *Zosterops* spp. from the Lake Matano area of southeast Sulawesi, Indonesia. Bulletin of the British Ornithologists' Club 105:136–139.

ICBP. 1992. Putting biodiversity on the map: priority areas for global conservation. International Council for Bird Preservation, Cambridge, United Kingdom.

Indrawan, M. and S. Somadikarta. 2004. A new species of hawk-owl from the Togian Islands, Gulf of Tomini, central Sulawesi, Indonesia. Bulletin of the British Ornithologists' Club 124:160–171.

Indrawan, M., Y. Masala, and L. Pesik. 1997. Recent observations in the Banggai Islands, Sulawesi. Kukila 9:61–71.

Indrawan, M., S. Somadikarta, J. Supriatna, M. D. Bruce, Sunarto, and G. Djanubudiman. 2006. The birds of the Togian Islands, Central Sulawesi, Indonesia. Forktail 22:7–22.

IUCN. 2001. IUCN red list of threatened species. 2001. Categories and criteria (Version 3.1). IUCN, Gland, Switzerland. www.redlist.org/info/categories_criteria2001.html (accessed 2 April 2006).

Mees, G. F. 1961. A systematic review of the Indo-Australian Zosteropidae (Part II). Zoologische Verhandlingen 50:1–168.

Owen, J. 2004. Mystery bird discovered on Indonesian island. National Geographic News. news.nationalgeographic.com/news/2004/01/0126_040126_wangiwangi.html (accessed 20 January 2006).

Rasmussen, P. C., J. C. Wardill, F. R. Lambert, and J. Riley. 2000. On the specific status of the Sangihe White-eye *Zosterops nehrkorni*, and the taxonomy of the Black-crowned White-eye *Z. atrifrons* complex. Forktail 16:69–81.

Slikas, B., I. B. Jones, S. R. Derrickson, and R. C. Fleischer. 2000. Phylogenetic relationships of Micronesian white-eyes based on mitochondrial sequence data. Auk 117:355–365.

Smithe, F. 1975. Naturalist's color guide. American Museum of Natural History, New York, USA.

Stattersfield, A. J., M. J. Crosby, A. J. Long, and D. G. Wege. 1998. Endemic bird areas of the world. BirdLife Conservation Series Number 7. BirdLife International, Cambridge, United Kingdom.

Warren, B. H., E. Bermingham, R. P. Prys-Jones, and C. Thébaud. 2006. Immigration, speciation and extinction in a highly diverse songbird lineage: white-eyes on Indian Ocean islands. Molecular Ecology 15:3769–3786.

Watling, D. 1983. Ornithological notes from Sulawesi. Emu 83:247–261.

White, C. M. N. and M. D. Bruce. 1986. The birds of Wallacea (Sulawesi, The Moluccas & Lesser Sunda Islands, Indonesia). An annotated checklist. B.O.U. Check-list Number 7. British Ornithologists' Union, London, United Kingdom.

The Wilson Journal of Ornithology 120(1):10–25, 2008

THE WHITE-EYED FOLIAGE-GLEANER (FURNARIIDAE: *AUTOMOLUS*) IS TWO SPECIES

KEVIN J. ZIMMER[1,2]

ABSTRACT.—New information on vocalizations of populations of the White-eyed Foliage-gleaner (*Automolus leucophthalmus*), and analysis of biometric and plumage characters, reveal that it consists of two biological species. One form is restricted to the Pernambuco Center of Endemism in coastal northeastern Brazil and the second occupies much of the remainder of humid Atlantic Forest from Bahia, Brazil south to northeastern Argentina and eastern Paraguay. The northeastern form, although cryptically similar morphologically to other subspecies of *Automolus leucophthalmus*, is highly differentiated in several vocal characters. The vocal difference between the two groups exceeds that between other accepted species pairs within the genus. Reciprocal tape-playback experiments offer supporting evidence that vocal differences within the White-eyed Foliage-gleaner complex are sufficient to act as isolating mechanisms in the event of secondary contact between the two groups. The northeastern form is shown to have vocal and morphological similarities to the Para Foliage-gleaner (*Automolus paraensis*) of southeastern Amazonian Brazil, supporting hypothesized Amazonian origins of the *leucophthalmus* complex, as well as a sister relationship with the *Automolus infuscatus/paraensis* complex. *Received 6 December 2006. Accepted 12 May 2007.*

The genus *Automolus* is a group of fairly large, mostly drab plumaged foliage-gleaners (subfamily Philydorinae), which, as currently recognized (Zimmer 2002, Remsen 2003), comprises eight species (*ochrolaemus*, *infuscatus*, *paraensis*, *leucophthalmus*, *melanopezus*, *roraimae*, *rubiginosus*, and *rufipileatus*). Members of the genus are distributed widely through tropical South America and Central America (Remsen 2003). The White-eyed Foliage-gleaner (*A. leucophthalmus*) has a disjunct distribution relative to all other congeners (which do not extend south of Amazonia), occurring in the Atlantic Forest region of eastern Brazil, eastern Paraguay, and northeastern Argentina (Remsen 2003). Originally described as *Anabates leucophthalmus* by Wied-Neuwied (1821) from specimens collected at Rio do Cachoeira, Bahia, Brazil, its range was subsequently considered to extend south through much of southeastern Brazil to Paraguay and Misiones, Argentina (Hellmayr 1925). Cory (1919) and Hellmayr (1925) noted that specimens of *leucophthalmus* from the southern part of the range were smaller and paler than those from Bahia. J. T. Zimmer (1947) reported the oldest name applicable to the smaller, paler birds from south of Bahia was *sulphurascens* (*Sphenura sulphurascens* Lichtenstein 1823). Concomitantly, he described a new subspecies, *lammi*, from a male collected at Recife, Pernambuco, Brazil by Donald Lamm. Subsequent authors (e.g., Peters 1951, Remsen 2003) followed Zimmer (1947) in recognizing *sulphurascens* and *lammi* as subspecies of *Automolus leucophthalmus*.

Andrew Whittaker and I were conducting field work in January 1996 in Alagoas, Brazil and noticed the local population of White-eyed Foliage-gleaners (*A. l. lammi*) varied dramatically in songs and calls from populations with which we were familiar in the Brazilian states of Espírito Santo, Rio de Janeiro, São Paulo, and Paraná. The songs of the Alagoas birds were more similar to those of birds then treated as *Automolus infuscatus paraensis* (Olive-backed Foliage-gleaner) of southeast Amazonia than they were of other populations of *A. leucophthalmus* (Zimmer 2002). I was intrigued by the vocal distinctiveness of birds that appeared, under field conditions, to be "typical" White-eyed Foliage-gleaners in plumage characters, and began investigating vocal and morphological variation among all of the recognized subspecies in the complex.

The objectives of this paper are to: (1) present new evidence of vocal differences among populations of White-eyed Foliage-gleaners, and (2) re-evaluate geographic variation in plumage and biometric characters within the

[1] Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, CA 90007, USA.

[2] Current address: 1665 Garcia Road, Atascadero, CA 93422, USA; e-mail: kjzimmer@charter.net

species. I demonstrate the subspecies *A. l. lammi* is sufficiently differentiated vocally to be considered a biological species distinct from other members of the group.

METHODS

I observed and tape recorded "White-eyed" Foliage-gleaners at sites throughout the Brazilian states of Alagoas, Pernambuco, Sergipe, Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina on multiple occasions from 1996 to 2006. All measurements used in behavioral data (distances, heights, etc.) are estimates. Mapped distributions are based on label data from specimens that I examined, and by more recent records documented with tape recordings. These localities, along with the type localities for each taxon, were entered into a geographic information system (Isler 1997) and mapped by M. L. Isler.

I assume that vocalizations of foliage-gleaners, like those of other suboscines, are mostly or entirely inherited (Kroodsma 1984, 1989; Kroodsma and Konishi 1991; Remsen 2003) and provide potentially important characters for systematic study (Lanyon 1978, Isler et al. 1997, Krabbe and Schulenberg 1997, Zimmer 1997). I assembled recordings of *Automolus leucophthalmus* from across its geographic range to analyze vocalizations (Appendix 1). Recordings were assigned to subspecies by location following the reported distribution of the three subspecies (*lammi*, *leucophthalmus*, *sulphurascens*) in current literature (Remsen 2003). I reviewed each recording to identify the number of individuals vocalizing and to label every vocalization as to type. Vocalizations were categorized as loudsongs, calls, and long calls for comparison. Loudsongs were consistently patterned multi-note vocalizations (Isler et al. 1997) given seemingly in the context of territorial advertisement. Vocalizations characterized as calls usually were structurally simple (typically involving well-spaced repetition of identical notes or pairs of notes), and most often were given in the context of contact notes between mates, or as aggression calls during territorial conflicts with conspecifics, or in response to tape playback. Vocalizations categorized as long calls were infrequently given series of mostly similar single note calls delivered in rapid succession, most often seemingly as signals of extreme agitation.

I made auditory comparisons of all recordings and visually compared spectrograms of all individuals of *A. l. lammi* and *A. l. leucophthalmus* recorded, as well as of a large, geographically balanced sample of recordings of *A. l. sulphurascens*. Songs selected for illustration as spectrograms were considered representative based on visual comparison of spectrograms of the large sample. I also examined my own collection of recordings of songs and calls of *A. rubiginosus*, *A. ochrolaemus*, *A. infuscatus*, *A. paraensis*, *A. rufipileatus*, and *A. melanopezus* for qualitative comparison with the vocalizations of *A. leucophthalmus*. This involved both auditory comparison and superficial visual comparison of spectrograms.

Visual (qualitative) characters were obtained through examination of printed copies of all spectrograms. I considered a character to be diagnostic visually when examination unambiguously distinguished one population from another. My tape recordings were made with a Sony TCM-5000 recorder with Sennheiser ME-80, ME-66, and MKH-70 shotgun microphones. Spectrograms used in illustrations were made by P. R. Isler, using Canary 1.2 and Raven 1.2 software (Bioacoustics Research Program, Cornell University Laboratory of Ornithology, Ithaca, NY, USA), Canvas graphics software (Version 5.0.3, Deneba Software, Miami, FL, USA), and a Hewlett Packard Laserjet 6MP printer.

Playback experiments were conducted to examine reactions of the three taxa currently considered subspecies of *A. leucophthalmus* to vocalizations of the other subspecies. In each case, an individual or pair of foliage-gleaners was first presented with a prerecorded tape of another taxon. Each taxon was represented for all trials by a single playback tape consisting of 10–15 songs interspersed with calls from three different individuals from three different localities. The *sulphurascens* tape contained recordings of individuals from Paraná, São Paulo, and Espírito Santo, Brazil. The *lammi* tape contained recordings of individuals from two sites in Alagoas and one in Sergipe, Brazil. The *leucophthalmus* tape contained vocalizations from two sites in Bahia. The tape of 10–15 songs plus calls was played during

each trial to conclusion. A buffer period of about 2 min was used to separate playback of vocalizations of different taxa to avoid confounding effects. Foliage-gleaners that did not respond to playback of other taxa were presented with a playback tape of their own vocal type. This was done to account for potential seasonal influences by resolving the question of whether birds that were unresponsive in the first trials were discriminating between the different vocalizations, or were generally nonterritorial during the trial period and therefore unresponsive to playback of any kind. Responses to playback were characterized as "strong," "moderate," "weak," or "none." A strong response involved immediate and repeated vocalizations (from previously nonvocalizing birds) as well as approach toward the sound source. A moderate response involved either a cautious approach without vocalizing, or sustained vocalizing without approach. A weak response involved single or unsustained vocalizations (from previously nonvocalizing birds) without approach. The none category includes instances in which birds remained silent (in the case of previously nonvocalizing birds) and did not approach the sound source, as well as instances in which already vocalizing birds neither changed the delivery or rate of their vocalizations, nor approached the sound source. A potential fifth category would be a "negative response," in which the subject responded to the sound stimulus by moving farther away. No negative responses to playback were observed from any taxa.

I examined representative specimens of *A. l. leucophthalmus* ($n = 5$), *A. l. sulphurascens* ($n = 32$), and *A. l. lammi* ($n = 6$) to identify morphological differences. These specimens are housed at the Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP); Field Museum of Natural History, Chicago (FMNH); Los Angeles County Museum of Natural History, Los Angeles (LACM); and the National Museum of Natural History, Washington, D.C. (USNM) (Appendix 2). A wing ruler with a perpendicular stop at zero was used to measure wing chord (wing) and tail length (tail) while dial calipers were used to measure tarsus length (tarsus), culmen length from the anterior end of the nares to the tip (culmen), bill depth at the anterior end of the nares (bill depth), and bill width at the anterior end of the nares (bill width). All measurements with calipers were to the nearest 0.1 mm; those taken with the wing ruler were to the nearest 0.5 mm. Measurement terminology conforms to Pyle et al. (1987). Plumage was described from specimens and compared to a standard color reference (Smithe 1975).

RESULTS

Distribution.—The distributions of the three subspecies of *Automolus leucophthalmus*, as ascertained from examination of specimens and tape recordings, varied (Fig. 1).

Habitat.—All forms of *Automolus leucophthalmus* occur in tropical lowland and foothill evergreen forest, and taller second-growth woodlands. All three subspecies occur near sea level. Nominate *leucophthalmus* was recorded to 750 m, *A. l. lammi* to 550 m, and *A. l. sulphurascens* to 900 m elevation.

Behavior.—All forms of *Automolus leucophthalmus* occupied the lower and mid levels of the forest strata. They were frequently, but not habitually, encountered as members of mixed-species flocks of insectivores comprised primarily of woodcreepers, other foliage-gleaners, antshrikes, and antwrens. The Red-crowned Ant-tanager (*Habia rubica*) appeared to be a nuclear species in most flocks in which *A. l. sulphurascens* occurred in São Paulo and Paraná. My observations of *A. l. lammi*, *A. l. sulphurascens*, and *A. l. leucophthalmus* suggest they are dead-leaf searching specialists (>75% of all foraging maneuvers involved searches of dead leaves for arthropods). Foliage-gleaners moved through vine tangles during these searches, going from one suspended dead leaf to another without scanning intervening live vegetation. Larger dead leaves were often vigorously pecked and pulled apart to get at arthropod prey concealed within the curls and folds. *A. l. sulphurascens* was observed on many occasions to rummage in leaves trapped in the bases of epiphytes, in the crowns of understory palms, and in the interiors of climbing bamboo thickets. Both *A. l. sulphurascens* and *A. l. lammi* were observed foraging to heights of 8–12 m, although most observations of all three forms were from much lower.

Plumage.—The three subspecies of White-eyed Foliage-gleaner are so similar in plumage characters that silent birds could easily

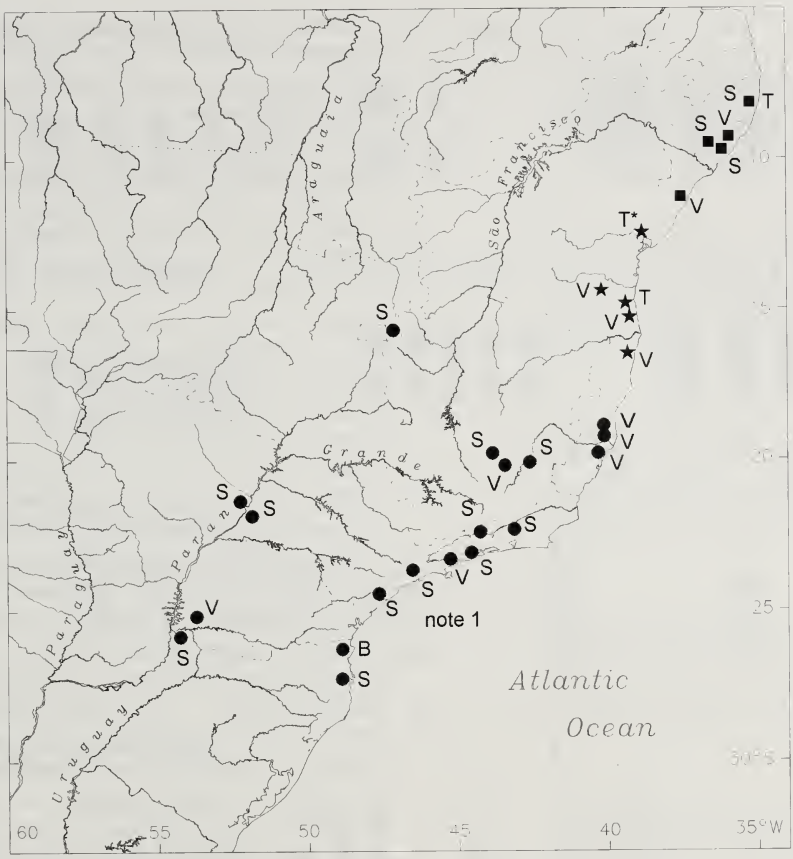


FIG. 1. Distribution of "White-eyed" Foliage-gleaners (*Automolus leucophthalmus*) confirmed by examination of specimens or tape recordings: stars = *A. l. leucophthalmus*; circles = *A. l. sulphurascens*; squares = *A. l. lammi* ; "T" next to a symbol indicates the type locality for that taxon; "S" next to a symbol indicates specimen confirmation for that taxon; "V" next to a symbol indicates vocal confirmation (tape recording) for that taxon; "B" next to a symbol indicates both specimen and vocal confirmation for that taxon; and "note 1" refers to a lack of a precise type locality for *A. l. sulphurascens*.

defy identification in the field. Specimens of *A. l. lammi* in direct comparison usually were separable from both *A. l. leucophthalmus* and *A. l. sulphurascens* by their darker and browner (less rufescent) dorsal color (closest to color #121A, Prout's Brown); darker and redder (less orange) tail (between color #34, Russet, and color #223A, Mars Brown); creamier (less white) throat; and dingier buff abdomen, which was brownest on the flanks, lower belly and vent (between color #239, Ground Cinnamon, and color #26, Clay Color, but closer to the latter). The two ANSP specimens of *A. l. leucophthalmus* were distinctly dirtier white on the throat (nearly grayish) with more reddish-brown on the lower flanks and abdomen than were any specimens of *A. l. sulphurascens*; these distinctions did not hold for the two USNM specimens of *A. l. leucophthalmus*.

Size.—Measurements for the three subspecies of White-eyed Foliage-gleaner varied (Table 1). Gender of four of the five specimens of nominate *leucophthalmus* was unknown and measurements for that taxon are not divided by male or female.

Vocalizations.—I assembled recordings of 103 different White-eyed Foliage-gleaners (17 *leucophthalmus*, 68 *sulphurascens*, and 18 *lammi*), including 844 individual songs (75 *leucophthalmus*, 523 *sulphurascens*, and 246 *lammi*) and 2,058 individual calls and long calls (771 *leucophthalmus*, 992 *sulphurascens*, and 295 *lammi*).

TABLE 1. Means ± SD (ranges) of selected measurements (mm) of the three subspecies of White-eyed Foliage-gleaners (*Automolus leucophthalmus*). Sample sizes for each gender of each taxon are in parentheses, except for nominate *leucophthalmus*, in which genders of specimens were not identified.

Taxon	Gender (*n*)	Culmen	Bill depth	Bill width	Wing	Tarsus	Tail
leucophthalmus	Unknown (5)	14.2 ± 0.7 (13.0–14.7)	6.4 ± 0.3 (6.1–6.8)	4.9 ± 0.1 (4.7–5.0)	92.4 ± 1.8 (90–94)	24.0 ± 0.9 (22.6–24.7)	83.4 ± 3.6 (80–89)
sulphurascens	Males (17)	14.2 ± 0.5 (13.5–15.4)	6.3 ± 0.3 (5.8–6.9)	4.7 ± 0.3 (4.4–5.0)	87.4 ± 2.9 (83.5–93)	23.7 ± 0.8 (22.2–25.2)	83.6 ± 4.2 (79–96)
	Females (11)	13.9 ± 0.7 (12.7–14.8)	6.1 ± 0.4 (5.4–6.8)	4.8 ± 0.2 (4.4–5.3)	85.2 ± 3.0 (80–91.5)	23.5 ± 0.8 (22.5–24.9)	82.5 ± 3.7 (78–91)
lammi	Males (4)	14.9 ± 0.9 (13.6–15.9)	6.6 ± 0.3 (6.2–6.8)	4.8 ± 0.5 (4.1–5.2)	91.4 ± 4.3 (85–94)	24.4 ± 0.7 (23.8–25.4)	82.0 ± 3.9 (78–87)
	Females (2)	14.7 ± 1.4 (13.8–15.7)	7.0 ± 0.5 (6.6–7.3)	5.4 ± 0.8 (4.9–6.0)	89.3 ± 1.0 (88.5–90)	23.7 ± 0.7 (23.2–24.2)	80.8 ± 1.1 (80–81.5)

Spectrographic analysis confirmed my field impressions that *A. l. lammi* differed strikingly and consistently in its loudsongs from both *A. l. sulphurascens* and *A. l. leucophthalmus*. The loudsong of this subspecies (Fig. 2A–F) was a countable series of 2–11 closely spaced (3–4/sec), frequency-modulated notes or doublets, each of which had a particularly harsh, grating quality. Doublets were formed by the close pairing of harsh notes with sharp thin notes. The sharp notes were seldom discernable in the field, except at close range when they were at times apparent as a sharp "hiccup" prior to the first note of a song. However, they are clearly visible in some spectrograms (Fig. 2D) as chevron-shaped notes preceding each frequency-modulated note. The frequency-modulated notes are readily identified in the spectrograms because they cover a wide band width (the difference between the highest and lowest frequency within a note, either at a given point in time or over the entire course of the note), and produce a trace that resembles a "zig-zag" sewing machine stitch within the confines of the general shape of the note. The frequency-modulated notes in *A. l. lammi* songs appear as rectangular-shaped or as shallowly inverted-U-shaped notes in the spectrograms. They have a distinctive strident quality to the human ear and it was this quality that allowed immediate identification of *A. l. lammi* songs in the field.

The number of notes and length of songs varied within a song bout in the same individual. Typical songs contained 3–6 notes or doublets (92% of all songs) with 4 notes/doublets being most common (35% of all songs). Individuals within a song bout tended to sing 3–5 consecutive songs with an identical number of notes before adding or subtracting notes. Twelve of 15 individuals for which loudsongs were recorded varied the number of notes/doublets per song within a recorded song bout. Responses to playback were within the same range of notes found in natural (unsolicited) songs. The peak frequency pattern within the songs was flat; that is, peak frequencies of successive notes in the song were roughly equal with little rise or fall. Occasional loudsongs contained a well-differentiated, longer first doublet (Fig. 2C), but these were the exception. *Automolus* species are sexually monochromatic and both males and

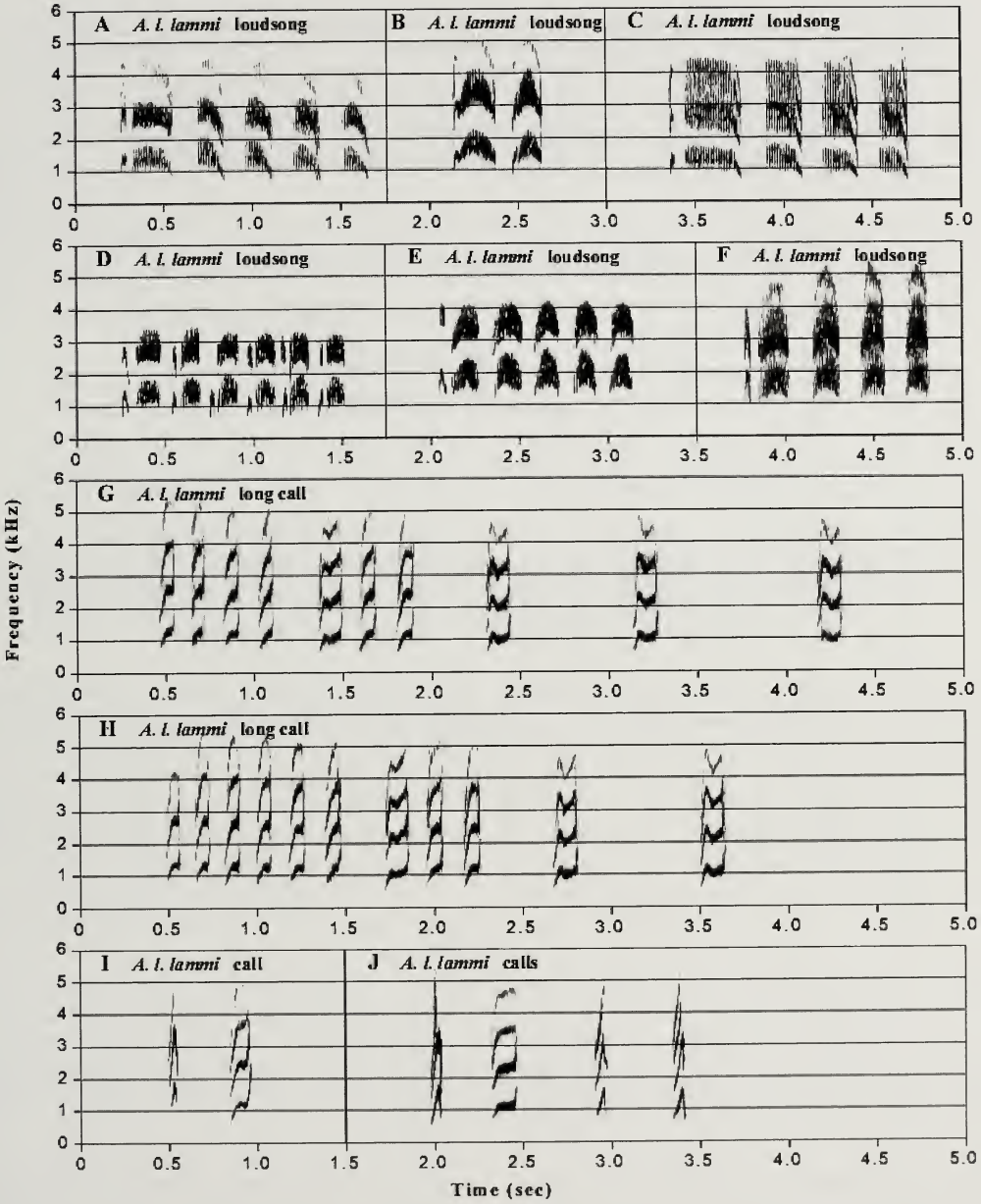


FIG. 2. Types of vocalizations of *Automolus leucophthalmus lammi*: (A) loudsong from Sergipe, Brazil; (B) short loudsong from Sergipe, Brazil; (C) loudsong from Sergipe, Brazil; (D) loudsong from Alagoas, Brazil; (E) loudsong from Alagoas, Brazil; (F) loudsong from Alagoas, Brazil; (G) long call from Sergipe, Brazil; (H) long call from Sergipe, Brazil; (I) two-note call from Alagoas, Brazil; and (J) two-note and one-note calls from Sergipe, Brazil. All spectrograms from recordings by K. J. Zimmer.

females sing; thus, the sexual identity of singing birds could not be ascertained. However, when presumed mated pairs responded to playback, the songs of each member of the pair were similar in pattern and quality to one another, and differed only slightly in peak frequency.

The loudsongs of *A. l. sulphurascens* (Fig. 3A–D) in contrast, consisted of a barely countable, faster-paced (5–7 doublets/sec) se-

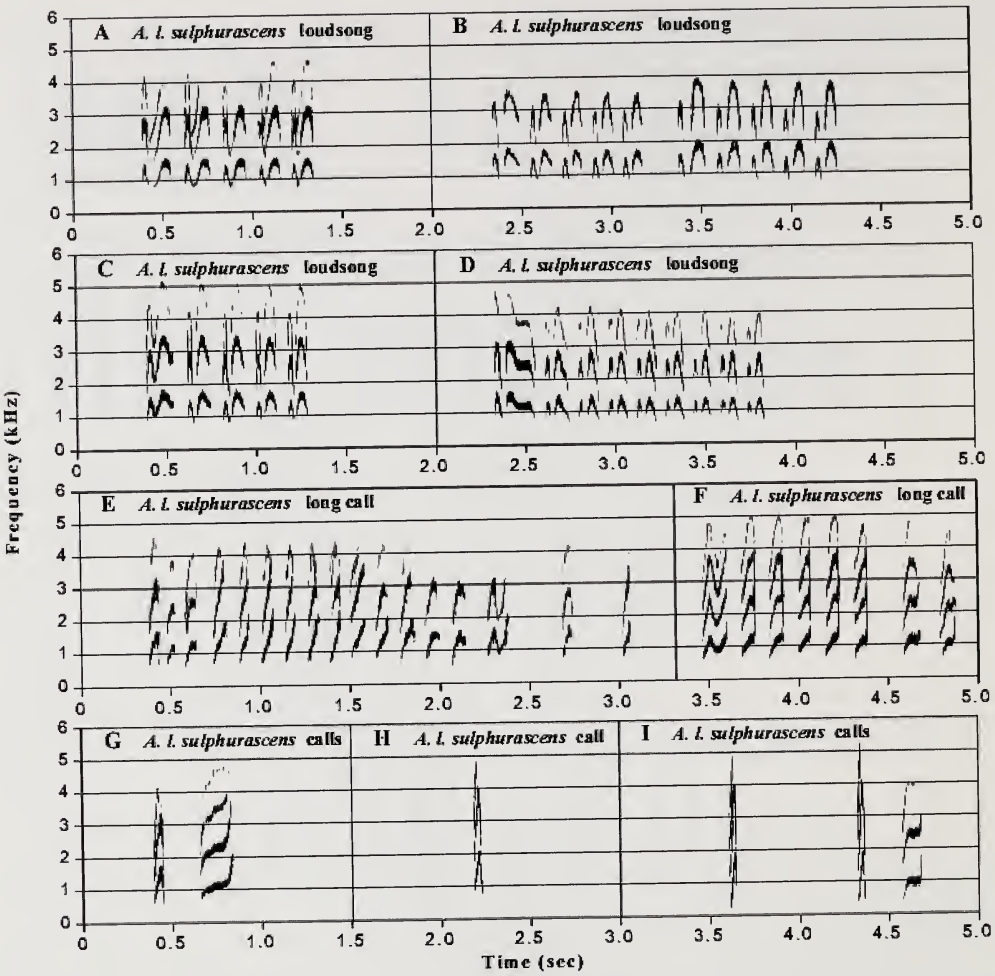


FIG. 3. Types of vocalizations of *Automolus leucophthalmus sulphurascens*: (A) loudsong from Ubatuba, São Paulo, Brazil; (B) loudsongs of presumed mated pair from Ubatuba, São Paulo, Brazil; (C) loudsong from Iguaçu, Paraná, Brazil; (D) loudsong from Linhares, Espírito Santo, Brazil; (E) long call from Ubatuba, São Paulo, Brazil; (F) long call from Linhares, Espírito Santo, Brazil; (G) two-note call from Ubatuba, São Paulo, Brazil; (H) one-note call from Ubatuba, São Paulo, Brazil; and (I) one-note and two-note calls from Iguaçu, Paraná, Brazil. All spectrograms from recordings by K. J. Zimmer.

ries of 2–12 closely spaced doublets. The individual notes which were clear in tone lacked the frequency modulation that defined the component notes of *A. l. lammi* loudsongs. The doublets of *A. l. sulphurascens* loudsongs consisted of two closely paired chevron-shaped notes, the second of which was typically higher in peak frequency than the first and longer in length. Visually diagnostic differences in note shape and clarity (frequency-modulated vs. clear) between the two taxa were apparent in all spectrograms. Loudsongs of *A. l. sulphurascens*, as with *A. l. lammi*, exhibited a fairly flat peak frequency pattern and only occasionally (Fig. 3D) had well-differentiated, longer introductory doublets.

The number of notes and the length of loudsongs in *A. l. sulphurascens*, as with *A. l. lammi*, varied within a song bout in the same individual. Typical loudsongs contained 4–9 doublets (94% of all songs) with 5 doublets being most common (31% of all songs). Individuals within a song bout tended to sing 3–5 consecutive loudsongs with an identical number of notes before adding or subtracting notes. Forty-nine of 51 individuals for which

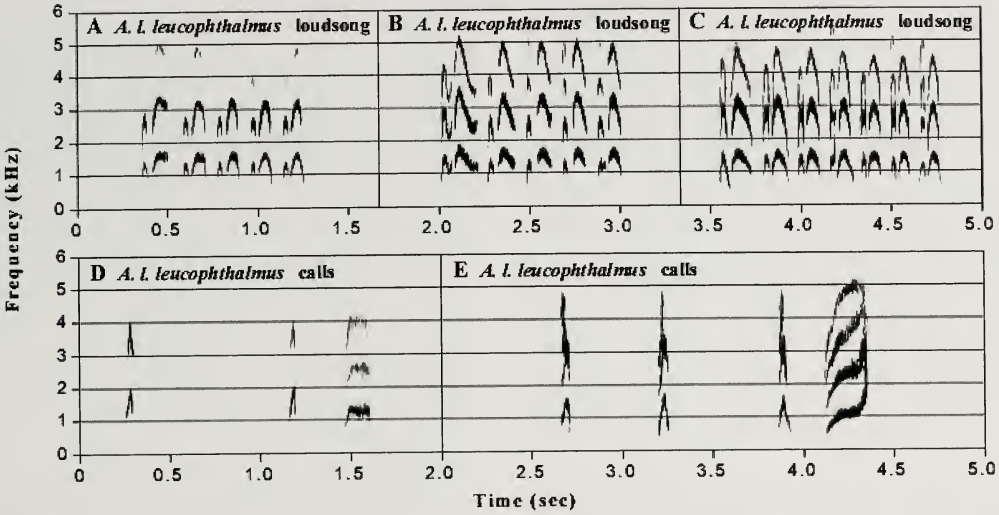


FIG. 4. Types of vocalizations of *Automolus leucophthalmus leucophthalmus*: (A) loudsong from Pto. Seguro, Bahia, Brazil; (B) loudsong from Fazenda Palmeiras, Bahia, Brazil; (C) loudsong from Fazenda Palmeiras, Bahia, Brazil; (D) one-note and two-note calls from Pto. Seguro, Bahia, Brazil; and (E) one-note and two-note calls from Fazenda Palmeiras, Bahia, Brazil. All spectrograms from recordings by K. J. Zimmer.

loudsongs were recorded varied the number of doublets per song within a recorded song bout. Responses to playback were within the same range of notes in natural (unsolicited) loudsongs. Males and females of presumed mated pairs sang nearly identical loudsongs that differed only slightly in note shape and mean peak frequency (Fig. 3B).

The smaller sample (10 individuals; 75 total songs) of *A. l. leucophthalmus* loudsongs (Fig. 4A–C) was visually indistinguishable in note shape, clarity, and peak frequency pattern from those of *A. l. sulphurascens*. Loudsongs of nominate *leucophthalmus* consisted of 2–8 closely spaced doublets with typical loudsongs containing 4–8 doublets (96%) and 5-doublet loudsongs being most common (33%). Seven of 10 individuals for which loudsongs were recorded varied the number of doublets per song within a recorded song bout.

Long calls also differed noticeably between *A. l. lammi* and *A. l. sulphurascens*. Long calls were highly variable between and within individuals of the same subspecies. Most of the variation involved the number of notes (8–20) which, in turn, often was seemingly influenced by extent of agitation. Birds that were particularly upset typically gave longer calls. Long calls of *A. l. lammi* consisted of a series of loud, slightly liquid sounding *weck* notes, the first several of which were closely and evenly spaced, followed by a slight gap and then another shorter cluster of notes before tailing off with two or more widely spaced individual notes (Fig. 2G–H). Notes in the terminal half of these long calls were longer and more drawn-out (*weck weck weck weck weck weckk weckk weckk weckkk weckkk).* In spectrograms, the shape of these terminal notes appears as a letter "Z" turned on its side, whereas the introductory notes appear more as inverted check marks with the longer tail at the beginning of the note (Fig. 2G–H). Long calls of *A. l. sulphurascens* typically began with a prelude of 1–3 differentiated notes that rose and fell in frequency and then settled into an uncountable series of 5–10 identical, closely-spaced notes, before decreasing in frequency and slowing in pace with two or more slightly differentiated terminal notes (Fig. 3E–F). The variation in frequency of the introductory notes imparted the effect of a sputtering gas motor just before it begins to burn on all cylinders. No prelude was apparent in long calls of *A. l. lammi*, whose component notes showed a nearly flat frequency pattern over the duration of the call. Note shapes varied visibly between the two subspecies. Both forms had elements that appeared on spectro-

grams as inverted check-marks or chevrons, but in *A. l. lammi* the tops of these note-tracings are more rounded and open, whereas in *A. l. sulphurascens* they appear as more pointed and closed. The difference is apparent to the human ear with the notes of *A. l. lammi* sounding more liquid in quality, whereas those of *A. l. sulphurascens* sound sharper. Some long calls of *A. l. sulphurascens* also contained several strongly upslurred notes whose tracings appear as nearly vertical sweeps lacking any tail (Fig. 3E); no similar notes were apparent in long calls of *A. l. lammi*. The limited sample of *A. l. leucophthalmus* recordings lacked long calls for comparison.

Other calls of the three subspecies were more similar. All three subspecies frequently gave single-note *kwek* calls and double-noted *kwek-kwaah* calls (Figs. 2I–J, 3G–I, 4D–E), mostly as contact calls between separated pair members, but also as agonistic calls in response to tape playback. Both members of presumed mated pairs gave nearly identical calls which, if anything, differed only slightly in pitch. These vocalizations were reminiscent in quality to calls of species of *Synallaxis* spinetails (e.g., *Synallaxis rutilans*) as well as those of the Olive-backed Foliage-gleaner (*Automolus infuscatus*) (K. J. Zimmer, tape recordings).

Tape Playback Experiments.—Playback experiments with recordings of *Automolus* offer further evidence of the significance of vocal differences among the taxa and their role as potential isolating mechanisms. I performed tape playback experiments on 32 individuals or pairs of *sulphurascens* in Paraná (12 in Sep 2003, 6 in Oct 2004, and 3 in Sep 2005) and Espírito Santo (7 in Oct 2003 and 4 in Oct 2004), Brazil. All birds were first presented with recordings of *lammi*. None of the 32 individuals or pairs of *sulphurascens* indicated any response to tape playback of vocalizations of *lammi*. Birds were next presented with recordings of nominate *leucophthalmus*. Thirty of 32 individuals or pairs of *sulphurascens* responded strongly to tape playback of *leucophthalmus* vocalizations and, in each instance, these same individuals and pairs responded strongly to playback of *sulphurascens* vocalizations as well. Birds responded in each case by vocalizing immediately followed by direct and rapid approach toward the sound source. Birds that were already vocalizing prior to playback invariably switched to a different vocalization, either from loudsongs to calls, or from calls to loudsongs, and frequently delivered a long call. In two instances (both in Paraná), individuals or pairs failed to respond to tape playback of any *Automolus* vocalizations. The birds involved on both occasions were moving with mixed-species understory flocks, and may have moved beyond the broadcast range of my tape recorder by the time I had completed playback of *lammi* vocalizations and commenced playback of *leucophthalmus* vocalizations.

I performed tape playback experiments on six individuals or pairs of *lammi* in Sergipe (2 in Jan 2004) and Alagoas (4 in Jan 2004), Brazil. All birds were first presented with recordings of nominate *leucophthalmus* followed by recordings of *sulphurascens*. None of the six pairs or individuals indicated any response to either *leucophthalmus* or *sulphurascens* vocalizations. Birds were then presented with recordings of their own vocal type. Five of six individuals or pairs responded to playback with an immediate vocal response followed by direct and aggressive approach toward the sound source. Already vocalizing birds, as was the case in the *sulphurascens* trials, changed their vocalization to a different type and frequently gave long calls when responding to playback. One individual failed to respond to playback of any kind, even when it was in full view <20 m distant.

Tape playback experiments were conducted on six individuals or pairs of *leucophthalmus* in Bahia, Brazil in February 2006. All birds were first presented with recordings of *lammi* followed by recordings of *sulphurascens* and nominate *leucophthalmus*. None of the six pairs or individuals indicated any response to playback of *lammi* recordings. Birds responded strongly in each instance to playback of *sulphurascens* and *leucophthalmus* recordings with immediate vocal response followed by direct and aggressive approach toward the sound source.

DISCUSSION

Spectrographic comparison of vocal characters reveals that *Automolus leucophthalmus lammi* differs dramatically in several aspects

of its vocal repertoire from all other populations in the complex. The loudsongs of *A. l. lammi* differed diagnosably from loudsongs of the other two taxa in two visual characters: the shape of all individual notes, and in being strongly frequency modulated. Both distinctions are clearly evident in all spectrograms. Loudsongs of *A. l. lammi* were also consistently slower paced than those of the other subspecies, as evidenced by the obviously longer between-note intervals visible in the spectrograms. Differences in the long calls of *A. l. lammi* from those of *A. l. sulphurascens* were less striking, but still substantial, and included differences in individual note shape throughout the calls, flatter peak frequency pattern, and absence of well-differentiated introductory and terminal notes, all characters that were visually diagnostic in all spectrograms. Isler et al. (1998) compared vocal characters between eight pairs of syntopic antbird (Thamnophilidae) species and found that within each species-pair, the members were diagnosable in a minimum of three different characters of the loudsong and calls. This standard is exceeded in a comparison of vocal differences between *A. l. lammi* and *A. l. sulphurascens/leucophthalmus*. The syntopic antbird study and those subsequent (e.g., Isler et al. 2001, 2002, 2005) incorporated use of visually diagnostic characters (including note shape, presence or absence of frequency modulation, note shape pattern, and peak frequency pattern) obtained from spectrograms as diagnosable differences in assessing species limits.

The vocal distinctions between *A. l. lammi* and other White-eyed Foliage-gleaners are even more noteworthy when the lack of geographic variation within the remainder of the complex is considered. Tape recordings of *A. l. sulphurascens* from Iguaçu, Paraná, (across the Rio Iguaçu from Misiones Province, Argentina) and from Itapoá, Santa Catarina, both near the southern boundaries for the species, were indistinguishable from those of *sulphurascens* from northern Espírito Santo (near the northern geographic limit of *sulphurascens*) and from those of nominate *leucophthalmus* from Bahia. Remsen (2005), in his overview of the use of vocal characters in assessing questions of species limits, made it clear that broad geographic sampling from throughout a species' range (not just from the endpoints) is needed. My inventory of White-eyed Foliage-gleaner recordings nearly spanned the north-south and east-west boundaries of the known range with representative recordings from many points in between.

The biological and taxonomic significance of these vocal distinctions is suggested by the results of the playback experiments. Sample sizes were small for two of the pairwise tests, but those performed were unequivocal. None of the *A. l. sulphurascens* or *A. l. leucophthalmus* tested showed any response to repeated playbacks of *A. l. lammi*, nor did any of the *A. l. lammi* respond to playbacks of either *A. l. sulphurascens* or *A. l. leucophthalmus*. One of the frequent criticisms of the experimental design and subsequent interpretation of playback experiments is failure to account for seasonal differences in responsiveness (Kroodsma 1986, Remsen 2005). This possibility was accounted for in my playback trials when over 93% of all birds tested (30 of 32 *A. l. sulphurascens*, 6 of 6 *A. l. leucophthalmus*, and 5 of 6 *A. l. lammi*) responded strongly to playback of their own vocal types, after ignoring playbacks of one or more of the other taxa. The lack of response from any taxon to songs of one of the others was not due to a seasonal lack of interest in territorial defense.

The extent of divergence in vocal characters between *lammi* and the other two taxa greatly exceeds that of morphological divergence. Although *lammi* is larger than *sulphurascens* in several mensural characters (particularly culmen length), there is overlap in the ranges of most characters, and nominate *leucophthalmus* is similar in most measurements to *lammi*. Similarly, although plumage characters can allow separation of specimens with direct comparison, their utility in the field is uncertain at best. The lack of plumage distinctions between forms that are so different vocally should not be unexpected as the Furnariidae are known for their remarkable homogeneity in coloration (Remsen 2003). Recent studies of neotropical suboscine passerines have revealed numerous cases of cryptic biodiversity in which distinct species-level taxa with dramatically different vocalizations were long overlooked because of their morphological similarity to more widespread forms (e.g., Pierpont and Fitzpatrick 1983,

Willis 1992a, Bierregaard et al. 1997, Krabbe and Schulenberg 1997, Zimmer et al. 2001).

The distribution of *A. l. lammi* as a species-level taxon distinct from other members of the complex is consistent with demonstrated biogeographic patterns. The entirety of its range is included in the Sierra do Mar center of endemism as defined by Cracraft (1985) and the southeastern Brazil center of endemism as defined by Haffer (1985), areas which essentially include the entire ranges of *A. l. leucophthalmus* and *A. l. sulphurascens*. However, Cracraft (1985:72) noted that "This center will surely be subdivided into smaller subcenters when bird distributions are examined in more detail." Other authors (Müller 1973, Jackson 1978, Kinzey 1982) had already recognized (based partly on the distribution of primate and reptile taxa) three to four separate, smaller centers of endemism from coastal Brazil, one of which is the narrow belt of coastal and montane forests lying north of the Rio São Francisco, usually referred to as the "Pernambuco Center". Thirty-eight bird taxa (including *A. l. lammi*) have been recognized as endemic to the Pernambuco Center (Silveira et al. 2003). Stattersfield et al. (1998: 277), in their compilation of "endemic bird areas (EBAs)", recognized the "Atlantic Slope of Alagoas and Pernambuco" as an EBA comprising the Atlantic coastal forest in northeast Brazil, primarily in Pernambuco and Alagoas, the primary habitat of which is tropical evergreen forest. A distinct group of endemic, range-restricted birds (*Philydor novaesi*, *Myrmotherula snowi*, *Terenura sicki*, and *Phylloscartes ceciliae*) that are confined to tropical evergreen forests in Alagoas and Pernambuco, primarily above 500 m, occur within this EBA. Three of these four species, all of which occur syntopically with *A. l. lammi* in portions of its limited range, have a pattern of geographic replacement by their presumed closest relatives (*Philydor atricapillus*, *Myrmotherula unicolor*, and *Terenura maculata*, respectively) in the Atlantic coastal forests between southern Bahia and northern Rio de Janeiro (Remsen 2003, Zimmer and Isler 2003). This essentially parallels the replacement of *A. l. lammi* by *A. l. leucophthalmus* and *A. l. sulphurascens*.

Spectrographic and auditory comparison of vocal characters throughout *Automolus* suggests a close relationship between all members of the *A. leucophthalmus* complex and both *A. infuscatus*, the Olive-backed Foliage-gleaner, and *A. paraensis*, the Para Foliage-gleaner (Zimmer 2002). Single-note calls, double-note calls, and long calls of all three species are more similar to one another than they are to homologous vocalizations of other *Automolus* species (K. J. Zimmer, recordings). Loudsongs of *A. paraensis* are also similar in pattern to those of all members of the *A. leucophthalmus* complex and share with *A. l. lammi* the distinctive, frequency-modulated strident notes that are otherwise unique within the genus (Zimmer 2002). Willis (1988a) suggested a possible superspecies relationship between *A. leucophthalmus* and *A. infuscatus* based on certain vocal similarities, but did not elaborate. In the type description of *lammi*, Zimmer (1947:101) stated that: "The more extensively shaded and darker bill of this form may possibly indicate a trend toward *Automolus infuscatus*, one form of which, *paraensis*, occurs in the Pará district of eastern Brazil. The darker and duller hues of the general coloration may possibly point in the same direction, but there is still too great distinction between the two groups to justify specific union." Vaurie (1980), on the basis of morphological characters, also treated *A. leucophthalmus* and *A. infuscatus* as being more closely related to one another than to other members of the genus. More recently, Remsen (2003) proposed that *A. leucophthalmus* (including *lammi*) and *A. infuscatus* (including *paraensis*) formed a superspecies as suggested by voice, plumage pattern, and biogeography. The Pernambuco Center of Endemism has been considered an area of historical interchange between Amazonian and Atlantic Forest floral and faunal elements (Silveira et al. 2003). Willis (1992b:7), in discussing the possible Amazonian origins of Atlantic Forest taxa, specifically suggested a "northern crossing" in the Pernambuco region as a point of origin for *Automolus leucophthalmus* based on the "Pernambucan subspecies [=*A. l. lammi*] showing some intermediate features to *A. infuscatus*." The vocal similarities between *A. l. lammi* and *A. paraensis* (formerly *A. infuscatus paraensis*), the geographically most proximate member of the *A. infuscatus* complex, lend further support to Willis' hypothe-

sis of an Amazonian origin for the White-eyed Foliage-gleaner complex and of the suggested sister relationship of the *infuscatus* group.

TAXONOMIC CONCLUSIONS

Automolus leucophthalmus lammi differs substantially in several characters of its loudsongs and long calls from the other subspecies in the complex. It also differs morphologically from the other members of the group, although these distinctions are subtle.

The extent of the vocal differences is more than sufficient to support the recognition of *A. l. lammi* as a separate species under any of the widely accepted species concepts (McKitrick and Zink 1988). The most difficult species concept to satisfy is the Biological Species Concept (BSC) because *A. l. lammi* is allopatrically or parapatrically distributed with respect to other members of the complex. A primary challenge in applying the BSC to allopatrically distributed taxa is the need to judge whether or not the taxa are sufficiently differentiated as to prevent extensive hybridization in the event of secondary contact. Johnson et al. (1999) advocated using the extent of differentiation between accepted biological species in the same genus as a measure for assessing whether a taxon has diverged sufficiently to be considered a separate species under the Biological Species Concept. Zimmer (2002) presented spectrographic comparisons of loudsongs of Chestnut-crowned (*Automolus rufipileatus*) and Olive-backed foliage-gleaners, two species widely sympatric in Amazonia, as an appropriate measure of species-level vocal differentiation within the genus. The loudsongs of *A. rufipileatus* and *A. infuscatus* were far more similar to one another than are the loudsongs of *A. l. lammi* to those of *A. l. leucophthalmus* and *A. l. sulphurascens* in note shape, note shape pattern, presence or absence of frequency modulation to notes, between-note intervals, and pace. Results of playback experiments offer supporting evidence that vocal differences within the White-eyed Foliage-gleaner complex are sufficient to act as isolating mechanisms in the event of secondary contact between the two groups (*lammi* vs. *leucophthalmus* and *sulphurascens*).

I could find no diagnosable differences between *A. l. leucophthalmus* and *A. l. sulphurascens*. The smaller sample of nominate *leucophthalmus* vocalizations were indistinguishable from the large sample of *sulphurascens* vocalizations. Biometrics and plumage data suggest that *leucophthalmus* is slightly larger and darker than *sulphurascens*, but clinal variation in the extent of color saturation within *sulphurascens* has been noted (Remsen 2003). The number of specimens of nominate *leucophthalmus* available was too small for either statistical analysis or meaningful qualitative generalizations. Until more specimens become available, I suggest that nominate *leucophthalmus* and *sulphurascens* continue to be treated as valid subspecies. Therefore, I submit the complex consists of two biological species:

Automolus lammi Zimmer–Pernambuco Foliage-gleaner
Automolus leucophthalmus (Wied-Neuwied)–White-eyed Foliage-gleaner
  A. l. leucophthalmus (Wied-Neuwied)
  A. l. sulphurascens (Lichtenstein)

The English name chosen for *A. lammi* highlights the Pernambuco Center of Endemism where the species is endemic, as well as one of the four Brazilian states to which it is restricted. I have chosen to retain the established name of "White-eyed Foliage-gleaner" as the English name for the other two taxa in the complex.

CONSERVATION IMPLICATIONS

The White-eyed Foliage-gleaner is uncommon to common throughout its range and is considered "not globally threatened" (Remsen 2003). Its range is more extensive than most Atlantic Forest endemics and includes a number of protected parks and reserves (Remsen 2003). Furthermore, it persists in taller second-growth woodlands, which also bodes well for its survival (Remsen 2003). This assessment pertains only to the widespread subspecies *sulphurascens*. Nominate *leucophthalmus* remains a poorly known bird from a handful of localities in Bahia (Remsen 2003). There are few specimens and, for most of these, the locality is given simply as "Bahia". It is almost certainly confined to the humid coastal plain and adjacent mountain ranges, but more work is needed to assess its northern and southern distributional limits and popu-

lation size, as well as to confirm its status as a distinct taxon relative to *sulphurascens*. It would be of particular interest to learn if the range of nominate *leucophthalmus* contacts that of *lammi* in northern Bahia or Sergipe.

Automolus lammi should be assigned the conservation status of "threatened" (Remsen 2003). Its known range is restricted to coastal Paraíba, Pernambuco, Alagoas, and Sergipe, all of which have suffered catastrophic loss of forest for agricultural purposes, primarily sugar-cane production. Brown and Brown (1992) estimated that only 2% of the original forest cover remained in Alagoas and Pernambuco states, and only 6% in Paraíba. Lowland forests in this region have been largely replaced by vast sugar-cane plantations with most remaining remnant forests restricted to steep slopes and ridge-tops (Stattersfield et al. 1998; KJZ, pers. obs.). Virtually all remaining forests in the region are true fragments, lacking even the narrowest of wooded corridors to other such fragments. Most of these exist on sugar-cane mill properties or *usinas*, rather than on formally protected lands (Silveira et al. 2003). This presents a particularly dire conservation picture for certain groups of forest-dependent birds with poor dispersal capabilities, many of which have been demonstrated to disappear from forest fragments below a minimum critical size, or in which anthropogenic activities such as selective logging are conducted. *Automolus* species have been shown to be among the most adversely affected birds by selected logging activities in French Guianan forests (Thiollay 1992) and by forest fragmentation in Amazonas, Brazil (Stouffer and Bierregaard 1995, Stouffer and Borges 2001).

Automolus lammi is known only from a few formally protected areas, notably from the privately owned Murici Biological Reserve and Pedra Talhada Federal Biological Reserve in Alagoas State. The former site has been identified as one of the most important sites for conservation in the Neotropics (Wege and Long 1995, BirdLife International 2000); despite its protected status, illegal selective logging of larger trees was an ongoing problem as recently as 2004 (pers. obs.). Recent surveys of privately owned forest fragments in the region found *A. lammi* in only a few sites and concluded that it appeared to be "genuinely rare" (Silveira et al. 2003:41). The same surveys found that *lammi* and other understory insectivores were inexplicably absent from some sites with seemingly suitable habitat. The authors suggested that widespread recent use of aerially dispersed pesticides in the surrounding *usinas* could be seriously impacting populations of insectivorous birds in the forest fragments.

Automolus lammi is only one of several distinctive avian taxa endemic to northeast Brazil in general, and the Pernambuco Center in particular, that have languished in relative obscurity due to their current taxonomic treatment as subspecies of broader-ranging species. Many of these forms, as noted by Silveira et al. (2003), were originally described as distinct species and later "lumped" into geographically widespread, polytypic species without analysis or even comment, as part of a generalized lumping trend in the mid 1900s. Recent fieldwork and preliminary investigations, particularly of vocal characters, suggests that many of these taxa merit recognition as distinct species under any of the widely recognized species concepts. The populations in question continue to suffer for our adherence to plumage-based taxonomies that greatly underestimate the true species-level biodiversity of tropical ecosystems. Other workers (e.g., Willis 1988b, 1991; Silveira et al. 2003) have reported the lack of attention given to conservation of endangered subspecies relative to endangered species, but the significance of this distinction cannot be overstated. Lack of understanding of species limits in widespread, polytypic groups, along with incomplete knowledge of distributions may result in serious underestimation of regional biodiversity and endemism, as well as obscuring historical patterns of biogeography and evolution. These miscalculations could have serious repercussions when decisions regarding allocation of scarce conservation dollars are considered.

ACKNOWLEDGMENTS

Special thanks are due M. L. and P. R. Isler for lending their time and talents in producing the map and spectrograms (respectively) for this paper. Andrew Whittaker was an enthusiastic partner in much of the fieldwork upon which this study was based. K. L. Garrett, K. C. Molina, and the staff at LACM were of inestimable help in coordinating specimen loans from

different institutions, as well as logistical support for the author's frequent museum visits. T. S. Schulenberg was available with helpful advice, and also provided access to several key references. I also thank J. M. Bates, S. J. Hackett, T. S. Schulenberg, and D. E. Willard (FMNH); S. L. Olson, G. R. Graves and Phillip Angle (USNM); and R. S. Ridgely and D. J. Agro (ANSP) for arranging specimen loans from their respective institutions. G. F. Budney, Andrea Priori, and the rest of the staff at the Library of Natural Sounds, Cornell Laboratory of Ornithology were of great help in providing access to the LNS collection of recordings. Andrew Whittaker and C. A. Marantz generously provided additional tape recordings to add to my inventory. I thank C. E. Braun, D. F. Stotz, and an anonymous reviewer for their many helpful comments on the manuscript. Special thanks go to Victor Emanuel Nature Tours, Inc. for providing me with many of the travel opportunities that made this research possible.

LITERATURE CITED

Bierregaard Jr., R. O., M. Cohn-Haft, and D. F. Stotz. 1997. Cryptic biodiversity: an overlooked species and new subspecies of antbird (Formicariidae) with a revision of *Cercomacra tyrannina* in northwestern South America. Ornithological Monographs 48:111–128.

BirdLife International. 2000. Threatened birds of the world. BirdLife International, Cambridge, United Kingdom and Lynx Edicions, Barcelona, Spain.

Brown Jr., K. S. and G. G. Brown. 1992. Habitat alteration and species loss in Brazilian forests. Pages 119–142 *in* Tropical forest and extinction (T. C. Whitmore and J. A. Sayer, Editors). Chapman and Hall, London, United Kingdom.

Cory, C. B. 1919. Descriptions of three new South American birds. Auk 36:540–541.

Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Ornithological Monographs 36:49–84.

Haffer, J. 1985. Avian zoogeography of the neotropical lowlands. Ornithological Monographs 36: 113–146.

Hellmayr, C. E. 1925. Catalogue of birds of the Americas. Part IV. Field Museum Natural History and Zoology Series 13:1–390.

Isler, M. L. 1997. A sector-based ornithological geographic information system for the Neotropics. Ornithological Monographs 48:345–354.

Isler, M. L., P. R. Isler, and R. T. Brumfield. 2005. Clinal variation in vocalizations of an antbird (Thamnophilidae) and implications for defining species limits. Auk 122:433–444.

Isler, M. L., P. R. Isler, and B. M. Whitney. 1997. Biogeography and systematics of the *Thamnophilus punctatus* (Thamnophilidae) complex. Ornithological Monographs 48:355–381.

Isler, M. L., P. R. Isler, and B. M. Whitney. 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). Auk 115:577–590.

Isler, M. L., J. Alvarez A., P. R. Isler, and B. M. Whitney. 2001. A new species of *Percnostola* antbird (Passeriformes: Thamnophilidae) from Amazonian Peru, and an analysis of species limits within *Percnostola rufifrons*. Wilson Bulletin 113: 164–176.

Isler, M. L., J. Alvarez A., P. R. Isler, T. Valqui, A. Begazo, and B. M. Whitney. 2002. Rediscovery of a cryptic species and description of a new subspecies in the *Myrmeciza hemimelaena* complex (Thamnophilidae) of the Neotropics. Auk 119:362–378.

Jackson, J. F. 1978. Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): implications for Pleistocene climatic changes in eastern Brazil. Arquivos de Zoologia (São Paulo) 30:1–79.

Johnson, N. K., J. V. Remsen Jr., and C. Cicero. 1999. Resolution of the debate over species concepts in ornithology: a new comprehensive biologic species concept. Proceedings of the International Ornithological Congress 22:1470–1482.

Kinzey, W. G. 1982. Distribution of primates and forest refuges. Pages 455–482 *in* Biological diversification in the Tropics (G. T. Prance, Editor). Columbia University Press, New York, USA.

Krabbe, N. and T. S. Schulenberg. 1997. Species limits and natural history of *Scytalopus* tapaculos (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. Ornithological Monographs 48:47–88.

Kroodsma, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24.

Kroodsma, D. E. 1986. Design of song playback experiments. Auk 103:640–642.

Kroodsma, D. E. 1989. Male Eastern Phoebes (*Sayornis phoebe*; Tyrannidae, Passeriformes) fail to imitate songs. Journal of Comparative Psychology 103:227–232.

Kroodsma, D. E. and M. Konishi. 1991. A suboscine bird (Eastern Phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. Animal Behavior 42:477–487.

Lanyon, W. E. 1978. Revision of the *Myiarchus* flycatchers of South America. Bulletin of the American Museum of Natural History 161:429–627.

Lichtenstein, M. H. K. 1823. Verzeichniss der Doubletten des Zoologischen Museums der Königl. Universität zu Berlin nebst Beschreibung vieler bisher unbekannter Arten von Säugethieren, Vögeln, Amphibien und Fischen // herausgegben von H. Lichtenstein. Zoologisches Museum: 41 [*Automolus leucophthalmus sulphurascens*], x + 118 pp. Berlin, Germany.

McKitrick, M. C. and R. M. Zink. 1988. Species concepts in ornithology. Condor 90:1–14.

Müller, P. 1973. Dispersal centers of terrestrial vertebrates in the neotropical realm. Biogeographica Number 2.

PETERS, J. L. 1951. Checklist of birds of the world. Volume VII. Harvard University Press, Cambridge, Massachusetts, USA.

PIERPONT, N. AND F. W. FITZPATRICK. 1983. Specific status and behavior of *Cymbilaimus sanctaemariae*, the Bamboo Antshrike, from southwestern Amazonia. Auk 100:645–652.

PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California, USA.

REMSEN JR., J. V. 2003. Family Furnariidae (ovenbirds). Pages 152–357 *in* Handbook of birds of the world. Volume 8. Broadbills to tapaculos (J. del Hoyo, A. Elliott, and D. Christie, Editors). Lynx Edicions, Barcelona, Spain.

REMSEN JR., J. V. 2005. Pattern, process, and rigor meet classification. Auk 122:403–413.

SILVEIRA, L. F., F. OLMOS, AND A. J. LONG. 2003. Birds in Atlantic Forest fragments in north-east Brazil. Cotinga 20:32–46.

SMITHE, F. B. 1975. Naturalist's color guide. American Museum of Natural History, New York, USA.

STATTERSFIELD, A. J., M. J. CROSBY, A. J. LONG, AND D. C. WEGE. 1998. Endemic bird areas of the world. Priorities for biodiversity conservation. BirdLife Conservation Series 7. BirdLife International, Cambridge, United Kingdom.

STOUFFER, P. C. AND R. O. BIERREGAARD. 1995. Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76:2429–2445.

STOUFFER, P. C. AND S. H. BORGES. 2001. Conservation recommendations for understory birds in Amazonian forest fragments and second-growth areas. Pages 248–261 *in* Lessons from Amazonia: the ecology and conservation of a fragmented forest (R. O. Bierregaard, C. Gascon, T. E. Lovejoy, and R. Mesquita, Editors). Yale University Press, New Haven, Connecticut, USA and London, United Kingdom.

THIOLLAY, J. M. 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. Conservation Biology 6:47–63.

VAURIE, C. 1980. Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). Bulletin of the American Museum of Natural History 166:1–357.

WEGE, D. C. AND A. J. LONG. 1995. Key areas for threatened birds in the Neotropics. BirdLife International Conservation Series 5. Cambridge, United Kingdom.

WIED-NEUWIED, M., PRINZ ZU. 1821. Reise nach Brasilien in den Jahren 1815 bis 1817 von Maximilian, Prinz zu Wied-Neuwied—mit zwei und zwanzig Kupfern, neunzehn Vignetten und drei Karten. Volume 2:141 [*Automolus leucophthalmus*]. Frankfurt am Main, Heinrich Ludwig Brönner, Germany.

WILLIS, E. O. 1988a. Behavioral notes, breeding records, and range extensions for Colombian birds. Revista de la Academia Colombiana de Ciencias 16:137–150.

WILLIS, E. O. 1988b. *Drymophila rubricollis* (Bertoni, 1901) is a valid species (Aves, Formicariidae). Revista Brasileira de Biologia 48:431–438.

WILLIS, E. O. 1991. Sibling species of greenlets (Vireonidae) in southern Brazil. Wilson Bulletin 103: 559–567.

WILLIS, E. O. 1992a. Three *Chamaeza* ant-thrushes in eastern Brazil (Formicariidae). Condor 94:110–116.

WILLIS, E. O. 1992b. Zoogeographical origins of eastern Brazilian birds. Ornitologia Neotropical 3:1–15.

ZIMMER, J. T. 1947. New birds from Pernambuco, Brazil. Proceedings of the Biological Society of Washington 60:99–106.

ZIMMER, K. J. 1997. Species limits in *Cranioleuca vulpina*. Ornithological Monographs 48:849–864.

ZIMMER, K. J. 2002. Species limits in Olive-backed Foliage-gleaners (*Automolus*: Furnariidae). Wilson Bulletin 114:20–37.

ZIMMER, K. J. AND M. L. ISLER. 2003. Family Thamnophilidae (typical antbirds). Pages 448–681 *in* Handbook of birds of the world. Volume 8. Broadbills to tapaculos (J. del Hoyo, A. Elliott, and D. Christie, Editors). Lynx Edicions, Barcelona, Spain.

ZIMMER, K. J., A. WHITTAKER, AND D. C. OREN. 2001. A cryptic new species of flycatcher (Tyrannidae: *Suiriri*) from the cerrado region of central South America. Auk 118:56–78.

APPENDIX 1

Recording locations and recordists.—Numbers following each name represent the number of individual birds recorded by the recordist at each site. All recordings are from Brazil. Capitalized names refer to Brazilian states. Only recordings of the taxa in the *Automolus leucophthalmus* complex and used in the vocal analysis are included. Recordings of other *Automolus* species were compared superficially.

Automolus l. lammi. ALAGOAS: Itabeguara (Zimmer 1); Murici Reserve (Zimmer 5, C. Marantz 3). SERGIPE: Crasto Reserve (Zimmer 9).

Automolus l. sulphurascens. ESPÍRITO SANTO: Caetés (Zimmer 2); Linhares CVRD Reserve (Zimmer 3); Augusto Ruschi Reserve (Zimmer 4); Santa Teresa (Zimmer 4); Sooretama Biological Reserve (Zimmer 1). MINAS GERAIS: Serra do Caraça Natural Reserve (Zimmer 2). PARANÁ: Iguaçu Falls National Park (Zimmer 33). SÃO PAULO: Ubatuba (Zimmer 17). SANTA

CATARINA: Volta Velha Reserve, Itapoa (Zimmer 2).

Automolus l. leucophthalmus. BAHIA: Boa Nova (A. Whittaker 1); Fazenda Palmeiras (Zimmer 12); Porto Seguro (Zimmer 2); Una Ecological Park (Zimmer 2).

APPENDIX 2

List of localities and lending institutions for specimens examined.—All specimens were from the following institutions: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania (ANSP); Field Museum of Natural History, Chicago, Illinois (FMNH); Los Angeles County Museum, Los Angeles, California (LACM); National Museum of Natural History, Washington, D.C. (USNM).

Automolus l. lammi (4 males, 2 females). BRAZIL: Engenho Riachão, Quebrangulo, Alagoas (LACM, 1 male); Usina Sinambú, Alagoas (LACM, 2 males, 2 females); Recife, Pernambuco (USNM, 1 male).

Automolus l. sulphurascens (18 males, 11 females, 3 unknown). ARGENTINA: Arroyo Urugua, Misiones (LACM, 1 male, 2 females). BRAZIL: Linhares, Espírito Santo (USNM, 1 male); Serra Dourada, Goiás (LACM, 1 male, 1 female, 1 unknown); Carrego Boa Esperanca, Mato Grosso (LACM, 1 male); Raul Seares, Minas Gerais (LACM, 3 males); Rio das Velhas, Minas Gerais (FMNH, 1 male); Parque Nacional de Itatiaia, Rio de Janeiro (LACM, 3 males, 1 unknown); Federal District, Rio de Janeiro (USNM, 1 female); Pedra Branca, Parati, Rio de Janeiro (LACM, 1 male, 2 females); Guapi, Rio de Janeiro (LACM, 1 male); Boa de Terezopolis, Rio de Janeiro (LACM, 2 males); Brusque, Santa Catarina (LACM, 1 female, 1 unknown); Joinville, Santa Catarina (FMNH, 1 female); Barra do Leapara, São Paulo (FMNH, 1 female); Costão dos Engenhos, São Paulo (FMNH, 1 male, 1 female); Paranapiacaba, São Paulo (FMNH, 1 male); Fazenda Bela Vista, Taquar, São Paulo (LACM, 1 male); Cantareira, São Paulo (LACM, 1 female).

Automolus l. leucophthalmus (4 unknown). BRAZIL: Bahia (USNM, 2 unknown; ANSP, 2 unknown); Espírito Santo (USNM, 1 male).

The Wilson Journal of Ornithology 120(1):26–37, 2008

RECENT ADVANCES IN THE BEHAVIORAL ECOLOGY OF TROPICAL BIRDS
The 2005 Margaret Morse Nice Lecture

BRIDGET J. M. STUTCHBURY[1,3] AND EUGENE S. MORTON[1,2]

ABSTRACT.—Tropical birds offer unique opportunities to test ecological and evolutionary theory because their life history traits are so diverse and different from temperate zone models upon which most empirical studies are based. We review recent studies on the behavioral ecology of tropical birds, studies that explore new advances in this field. Life histories and their evolution remain the focus of research on tropical birds. Clutch size manipulations in two species showed that food limitation does not explain small clutch size. In antbirds, enlarged clutches decreased post-fledging survival whereas in thrushes, enlarged broods were costly due to high nest predation. Small clutches may be favored via different ultimate selective forces and shared underlying tradeoffs between the immune, metabolic, and endocrine systems in the body may account for the commonly observed 'slow pace of life' in tropical birds. The physiological tradeoff between testosterone and immunocompetence may explain the evolution of low testosterone levels in tropical passerines where adult survival is paramount. In contrast to life history theory, few studies have explored temperate-tropical differences in territoriality, mating systems, and song function. The idea that low breeding synchrony in tropical birds is associated with low levels of extra-pair fertilizations was supported by several new paternity studies conducted on tropical passerines. Seasonally breeding tropical birds have higher testosterone levels than tropical birds with prolonged breeding seasons, although it is unclear if this pattern is driven by mating systems *per se* or selection from pathogens. Recent work on relations between pair members in permanently paired tropical passerines focuses on the question of mate defense versus territorial defense and the extent of cooperation versus selfish interests in inter-sexual relations. *Received 29 January 2007. Accepted 15 July 2007.*

Theory and empirical tests in the behavioral ecology of birds are generally constrained by a distributional problem. Whereas 80% of passerine birds reside in tropical latitudes, studies of temperate latitude species dominate our world view of avian biology. For example, does breeding occur when food for raising young is most abundant? Is the mating system of most passerine birds dominated by extra-pair behavior? Is song driven by sexual selection because it functions to attract mates for males? Does testosterone underlie the maintenance of aggression in territoriality? Well, this is what we think. But this is based on temperate passerines, popular test subjects for much of behavioral ecology theory. Studies of temperate birds outnumber those of tropical birds by a margin >100:1 (Stutchbury and Morton 2001).

What if an equivalent research effort had been spent on studying the same phenomena, but with birds in the tropics instead of birds in the temperate zone? Alexander Skutch (1985) provided a preview when he stated that the question of latitudinal clutch size variation should not be "why do tropical birds lay so few eggs?" but, rather "why do temperate zone birds lay so many?" Studies of tropical birds test existing theory, but they also lead to entirely new questions that would otherwise not be asked. Several years ago, we reviewed research on the behavioral ecology of tropical birds to show how run-of-the-mill tropical birds have fundamentally different adaptations for life history strategies, mating systems, territory defense, and communication (Stutchbury and Morton 2001). Here we highlight recent studies to illustrate how tropical birds can be used to test and develop new theories for understanding the evolution of bird behavior.

Temperate zone birds converge in their adaptations to the overwhelmingly huge and predictable temperature and resource swings of temperate latitudes, and the vast majority of temperate breeding passerines have highly seasonal territorial defense and breeding. This creates a high level of male-male competition for territories, an intense period of social mate choice, and a sudden rush of nesting and egg-

[1] Department of Biology, York University, 4700 Keele Street, Toronto, ON, M3J 1P3, Canada.

[2] Hemlock Hill Field Station, 22318 Teepleville Flats Road, Cambridge Springs, PA 16403, USA.

[3] Corresponding author; e-mail: bstutch@yorku.ca

laying activity among females. Thus, many temperate species face a common suite of selection pressures on breeding adaptations that are imposed by climate and short breeding season. Most tropical birds are free from the constraints of the spring rush to establish territories and find mates; they typically have access to mates, territories, and food year round. Many tropical birds, often both males and females, keep singing whether breeding or not, whereas temperate zone birds stop singing when breeding wanes and females sing in only a few species (Morton 1996). One might ask, in the Skutchian vein, not "why do so many female birds sing in the tropics?" but, rather, "why do so few females sing in the temperate zone?"

Temperate-tropical comparisons are fundamental to understanding the different selective pressures acting on birds, and have been applied most frequently to the question of life history evolution (Wikelski et al. 2003a, Tieleman et al. 2005). The great diversity in life histories among tropical birds should also be viewed as a resource, one that can be used to document the full evolutionary potential of avian adaptation. Within one study area it is straightforward to find tropical passerines that are highly seasonal breeders and others that are territorial and paired year-round and have a prolonged 6 to 8 month breeding season. Seasonal effects on food availability and breeding can occur even in the same forest, depending upon whether the species forages on the ground or in the bushes and vines above (Ahumada 2001). Similarly, in a single study site one finds species that breed in the dry season as opposed to the wet season, species in which males build nests and incubate eggs as opposed to only feeding young, and species in which adults rely primarily on fruit as opposed to insects. This diversity is the largely untapped resource offered by tropical birds, a powerful tool for testing behavioral ecology theory and developing new ideas that have a broad evolutionary scope (Stutchbury and Morton 2001). Our review focuses on recent advances in life history traits of tropical birds, their slow pace of life, their mating systems, and territoriality.

Life History Traits.—Tropical birds have a much smaller clutch size than their temperate zone counterparts, a fundamental latitudinal difference that has long been recognized (Skutch 1949), and still generates a great deal of theoretical and empirical study (Ghalambor and Martin 2001, Martin et al. 2001, Ricklefs and Wikelski 2002). There is little agreement, however, on whether small clutch sizes of tropical birds are favored because of food limitation, high predation risk, limited recruitment opportunities for juveniles, pathogens, or some combination of these selective factors (Ricklefs and Wikelski 2002). Clutch size manipulations have been a standard tool for testing optimal clutch size theory in temperate species, but few such experiments have been done with tropical birds (Stutchbury and Morton 2001).

Styrsky et al. (2005) experimentally reduced and enlarged clutches of Spotted Antbirds (*Hylophylax naevioides*) to created clutches of one, two, or three eggs. They found that parents of enlarged broods could successfully feed additional young by increasing their provisioning rate and the young fledged at normal weight. Furthermore, increased parental activity at the nest did not result in increased nest predation. Instead, the cost of having a large brood occurred after the young fledged by reducing juvenile survival. Broods of three had only 30% post-fledging survival compared with 70% for broods of one chick. Even natural broods of two eggs had lower juvenile survival (45%) than reduced clutches of one egg. Brood division after fledging normally results in each chick from a brood of two being cared for by a single parent. In enlarged clutches a single parent had to care for two chicks, but one of these chicks usually died in the first few days of the post-fledging period (Styrsky et al. 2005). This cost of a large clutch may be a general phenomenon because tropical passerines have a longer period of fledgling care and a longer delay before juvenile dispersal than temperate zone species (Russell et al. 2004).

Ferretti et al. (2005) manipulated clutch size in two populations of the Rufous-bellied Thrush (*Turdus rufiventris*) in subtropical Argentina to test whether lower food availability or high nest predation best explained interpopulation variation in average clutch size (3.2 vs. 2.7 eggs). Clutch size in both populations was experimentally standardized at three eggs, and manipulated so the eggs

hatched synchronously. If low food availability results in selection for small clutch sizes, one would predict the population with the smaller natural clutch size would experience low provisioning rates, slow nestling growth, and high starvation of nestlings. However, the opposite was true; the population with the larger initial clutch size apparently had less food available because nestlings experienced more starvation and slower growth rate. No starvation was observed in the population where clutches were enlarged, suggesting that food supply was not constraining clutch size. Instead, differences in nest predation (50 vs. 75%) appear to shape life history traits in this species because the population with the highest predation had small clutch sizes, longer incubation bouts, faster nestling growth, and lower parental visitation rates to the nest.

These two examples illustrate how the direct selective influence of environmental factors on clutch size can differ among species. We can also add to the mix an earlier clutch manipulation study on Clay-colored Thrushes (*Turdus grayi*) in Panama in which parents could not raise additional young during the dry season when there were abundant fruit resources for adults but arthropod food for nestlings was scarce (Stutchbury and Morton 2001). Clay-colored Thrushes bred at a poor time for feeding nestlings because predation was lower in the dry season (Morton 1971).

A comparative study of tropical passerines in Africa found that seasonality of food resources had a strong influence on life history traits (Peach et al. 2001). Nectarivores and insectivores had high survival (72%) and low clutch size whereas granivores had low annual survival (54%) and large clutch sizes. The unpredictable and highly seasonal rainfall, which directly affects seed availability, may reduce the survival of granivores and select for larger clutch sizes. The diversity of tropical avian adaptations to food availability is exemplified by a recent study of the endangered Hawaiian Akepa (*Loxops coccineus*) (Freed et al. 2007). This specialized bird, feeding only on insects and spiders in the foliage of ohia trees (*Metrosideros polymorpha*), illustrates "nestling overgrowth" where, at peak weight, nestlings weigh more than their parents. To attain this overgrowth, Akepa nestlings are fed more than they need thus banking this food for use during the 4-month fledgling period when food resources are declining. Akepa fledglings actually lose weight as they grow! Clay-colored Thrushes illustrate the opposite strategy. They fledge at much lower weights than the adult weight (e.g., at 35 vs. 80 g for adult weight) and continue to grow for long periods after fledging, even replacing remiges and rectrices in a complete molt so these will match their increasing size. Fledglings of the largest species of robin, the Great Thrush (*Turdus fuscater*) (33 cm long), are similar in size to fledgling robins of normal size for the genus (20–25 cm) but continue growing for an unknown length of time after fledging (E. S. Morton, unpubl. data).

Slow Pace of Life.—Tropical birds exhibit a lower basal metabolic rate than temperate birds (Wikelski et al. 2003a). Ricklefs and Wikelski (2002) argue that life history variation falls on a slow-fast continuum in all birds and that basic physiological tradeoffs can explain why tropical birds generally converge on one end of this continuum, despite a wide array of environments and selective forces. Under their model, different environmental factors act on separate physiological systems (immune, metabolic, and endocrine systems). Internal tradeoffs between the physiological systems result in a uniform life history (low clutch size, long life span) and 'slow pace of life' among tropical birds.

More resources may be allocated to adult survival than reproductive effort given a slow pace of life (Ricklefs and Wikelski 2002, Tieleman et al. 2005). Tropical birds appear to have a slower pace of life because they lay smaller clutches, hatchlings grow more slowly, and adults live longer than temperate zone birds, all of which suggest a lower resting metabolic rate (RMR) in tropical birds (reviewed in Wikelski et al. 2003a). The basic question is whether latitudinal relations between RMR are genetically based or whether local climate affects metabolic rates through acclimation. Weathers (1997) showed that RMR may vary by habitat in tropical birds with birds in open, sunny areas having higher metabolic rates than birds in shady forests. Eurasian Stone Chats (*Saxicola torquatus*) showed population-specific RMRs with birds from Kenya, Austria, Ireland, and Kazakhstan differing in RMR even though all were housed

under identical conditions in captivity. The tropical birds from Kenya had lower RMR (Wikelski et al. 2003b). They suggested that it was not migration or year-round territoriality but rather adaptation to temperature fluctuations that influences RMR. For example, birds from northern areas can experience cold temperatures during breeding and a higher RMR would be favored. The important point of the Eurasian Stone Chat study is that adaptation to local habitat may be under genetic control (Wikelski et al. 2003b).

A comparison of temperate-breeding and tropical House Wrens (*Troglodytes aedon*) found that Panamanian wrens had a lower field metabolic rate during reproduction, a smaller number of total provisioning trips to the nest (but not fewer trips per nestling), and fewer chicks per brood (Tieleman et al. 2006). Overall field metabolic rates during breeding were reduced by about 35% in tropical wrens, suggesting a slower pace of life, although some of this reduction may be the result of the much shorter day length in the tropics. In contrast to the temperate-breeding population, the tropical wrens did not show temporal variation in field metabolic rates while breeding which is likely due to their long breeding season.

The physiological tradeoff between testosterone and immune function is the best studied interaction among physiological systems that impacts life history evolution. This is often called the immunocompetence handicap hypothesis (Folstad and Karter 1992, Hillgarth and Wingfield 1997) and there is considerable variation among studies, and taxa, in the strength of evidence supporting this tradeoff (Roberts et al. 2004). Testosterone is important in the breeding biology of temperate male passerines, as plasma testosterone titers increase enormously during the breeding season and influence important reproductive processes such as song, courtship, sperm maturation, and territoriality (Balthazart 1983, Wingfield et al. 1990, Wingfield and Hahn 1994). Tropical birds, however, break this temperate zone rule because even during the peak of the breeding season males have low levels of testosterone (Levin and Wingfield 1992, Hau 2001). Testosterone plasma titers in temperate zone passerines are in the range of 2.1 to 5.5 ng ml^{-1}, whereas breeding tropical passerines have values such as 0.2 ng ml^{-1} in Spotted Antbirds (Hau et al. 2000) and 0.3 ng ml^{-1} in White-bellied Antbirds (*Myrmeciza longipes*) (Fedy and Stutchbury 2006). In Spotted Antbirds, brain sex steroid receptor expression is increased in the non-breeding season when testosterone levels are reduced (Hau 2007), a different pattern from temperate zone birds where circulating testosterone levels and sex steroid receptors are temporally linked (e.g., both highest during the breeding season). Traditional ideas about the role of testosterone in mediating aggression seem not to apply to tropical species, especially those with year-round territoriality (Wiley and Goldizen 2003).

The pace of life model proposes the great importance of immune function in tropical birds has a cascading effect; it reduces basal metabolic rate and reproductive effort to save energy and reduces testosterone to maintain immunocompetence, all of which result in a longer adult life span. The idea is that high testosterone can be tolerated in birds with short breeding seasons (e.g., temperate zone breeders) because the short time intervals alleviate the fitness-lowering effects of testosterone such as interference in parental care and possibly impaired immune function (Wingfield et al. 2001). Tropical birds that live at high altitudes may be able to sustain higher concentrations of testosterone than lowland birds because parasite loads are low in the highlands (Goymann et al. 2004). There is support for higher prevalence of hematozoan parasites in lowland than in highland tropical birds, but it may also be true that infections occur at a higher rate in temperate than in tropical birds, arguing against the tradeoff between testosterone and hematozoan prevalence as a causal factor underlying differences in the levels of testosterone (Ricklefs 1992, Durrant et al. 2006)

Even with almost undetectable levels of testosterone (Hau et al. 2000, Fedy and Stutchbury 2006), tropical male passerines vigorously defend territories, sing, attack intruders, and pair with females (Wikelski et al. 1999). Female tropical birds can be fiercely territorial yet have low testosterone levels (Levin 1996). It is not fully understood whether female aggression in general is mediated by testosterone (Ketterson et al. 2005) and studies of female

tropical birds would provide good subjects for resolving these questions. The general pattern for tropical passerines that defend territories throughout the year is low levels of testosterone during most of the year (Levin and Wingfield 1992, Hau et al. 2000, Wikelski et al. 2003b, Day et al. 2006, Fedy and Stutchbury 2006). Tropical birds may not be able to maintain high androgen levels due to their negative effects on immunocompetence and, instead, elevate testosterone only when needed; when territorial conflicts and instability arise (Wikelski et al. 1999). Testosterone did not increase in White-bellied Antbirds after simulated territorial intrusions or during temporary removal experiments that created territorial conflicts among males (Fedy and Stutchbury 2006).

If tropical birds have a slower pace of life, is it caused by a heightened immune function resulting from low levels of testosterone? Partial support for this causal relationship was found in House Sparrows (*Passer domesticus*). House Sparrows living in Panama laid smaller clutches over a long breeding season relative to a population in temperate New Jersey. Martin et al. (2006) found that in tropical House Sparrows, secondary antibody response to an administered novel antigen was faster and "energetic investment in immune activity" was greater than in temperate House Sparrows, as predicted by differences in pace of life. However, cell-mediated immune response was greater in the fast-living temperate birds. They concluded the relation of testosterone to a reduction in immune function is equivocal because different components of the immune system differ in their relative costs and benefits and only some differences may complement variation in life histories (Martin et al. 2006). Furthermore, a laboratory study of male House Sparrows from New Jersey found that testosterone did not suppress immune function during the nonbreeding season, so seasonal variation in immune function could not be explained by seasonal changes in testosterone levels (Greenman et al. 2005).

Comparisons of the role of testosterone in temperate and tropical populations of the Eurasian Stone Chat have been influential because of the depth of study in both field and captive situations. The Stone Chat has a large breeding range that includes migratory northern populations with a short breeding season to tropical populations that are resident and have year-long territoriality. Begun by Dittami and Gwinner (1985), the levels of testosterone and gonadal cycles have been studied recently in both the laboratory (Rodl et al. 2004) and in field situations (Goymann et al. 2006). Direct measurements of extra-pair mating behavior have not been published but the length of the breeding season and changes in testosterone suggest that extra-pair mating is common to all populations (Goymann et al. 2006). Stone Chats illustrate a reversal in breeding synchrony with temperate populations breeding over 5 months and tropical birds for a shorter period. Equatorial Stone Chats are single-brooded with individual pairs raising a clutch of three within a period of less than 3 months. Northern birds, in contrast, raise up to three clutches of five young each within a breeding season of 5–6 months (Helm et al. 2005, Schwabl et al. 2005). Equatorial Stone Chats, like other tropical birds, showed lower levels of testosterone (0.5 ng ml^{-1}or less) than their temperate counterparts, except during the stage when females were fertile (nest-building and laying), when testosterone levels were higher than those of European populations. This surge in testosterone was related to the relatively short time of female fertility (Goymann et al. 2006).

Another latitudinal comparison of testosterone has been accomplished within the genus *Zonotrichia*; northern populations of the White-crowned Sparrow (*Z. leucophrys*) and the tropical, but high altitude-living, Rufous-collared Sparrow (*Z. capensis*) (Moore et al. 2002, 2004a, 2004b; Wada et al. 2006). The tropical species of *Zonotrichia* can have levels of testosterone similar to northern latitude species (Moore et al. 2002). Moore et al. (2004a) report that testosterone in Rufous-collared Sparrows was higher during the main breeding period than the early breeding period (before incubation had begun), the opposite of the situation in the White-crowned Sparrow, whose testosterone levels are highest during territory establishment and decrease when they are feeding young (Morton et al. 1990). Rufous-collared Sparrows showed an elevated plasma testosterone when challenged by playbacks early in the breeding season. Oddly, testosterone was elevated much more in response

to playbacks of a heterospecific song (a sympatric seedeater) than by playback of the local conspecific dialect (4.2 vs. 2.0 ng ml^{-1})! Testosterone-implanted Rufous-collared Sparrows exhibited enhanced testosterone concentrations but were no more aggressive than blank-implanted controls (Moore et al. 2004a). The opposite experiment, blocking testosterone pharmacologically, also did not affect territorial aggression in Rufous-collared Sparrows (Moore et al. 2004b). Moore et al. (2004a) suggested that high altitude Rufous-collared Sparrows likely have an extra-pair mating system and the sustained levels of testosterone may reflect a genetically polygynous population where males would be favored to have elevated concentrations of testosterone throughout the breeding season (Moore et al. 2004a).

We predicted that high testosterone is due to competition for extra-pair fertilizations (EPFs) in birds (Stutchbury and Morton 2001), regardless of latitude, and this view is supported by recent reviews (Hirschenhauser et al. 2003, Goymann et al. 2004, Garamszegi et al. 2005). We emphasized that extra-pair mating systems result in increased male-male competition, but more than simply male/male aggression and territoriality. Part of the enhanced performance provided by testosterone likely includes influencing female choice of extra-pair mates. Studies of testosterone in birds to date have not been accompanied by study of the mating system and breeding synchrony of the target species, making it difficult to evaluate the relative roles of immune function and mating system.

Breeding Synchrony and Extra-pair Mating.—Breeding synchrony among fertile females is generally much higher for temperate breeding than tropical birds due to the dramatic differences in the length of the breeding season (Stutchbury and Morton 1995). For Nearctic-neotropical migrants, breeding synchrony (% of females simultaneously fertile) typically ranges from 20 to 40% among species (Stutchbury et al. 2005a). The breeding synchrony for tropical passerines studied to date ranges from 8 to 30% with most species <15% (Table 1). Low values are typical for species that are territorial and paired year-round with long breeding seasons, and the highest values (25–30%) occurred in species that defend seasonal territories and have a relatively short breeding season (Table 1).

TABLE 1. Frequency of extra-pair fertilizations and extent of breeding synchrony in socially monogamous tropical passerines. Values give % of extra-pair young and broods that contained at least one extra-pair young (sample size in parentheses), and the breeding synchrony index (Kempenaers 1993).

Species	EPF frequency, %		Breeding synchrony (%)
	Young	Broods	
Cercomacra tyrannina[a]	0 (15)	0 (12)	8
Tachycinita albilinea[b]	15 (98)	26 (30)	8
Elaenia flavogaster[c]	4 (24)	8 (13)	9–10
Thryothorus leucotis[d]	4 (53)	3 (31)	10
Zosterops lateralis[e]	0 (122)	0	12
Loxiodes bailleui[f]	0 (20)	0 (12)	low
Geospiza scandens[g]	8 (159)	15 (66)	low
Elaenia chiriquensis[h]	37 (14)	67 (15)	15–18
Turdus grayi[i]	38 (37)	53 (19)	25
Volatinia jacarina[j]	50 (20)	64 (7)	30

[a] Fleischer et al. 1997; [b] Moore et al. 1999; [c,h] Stutchbury et al. 2007; [d] Gill et al. 2005; [e] Robertson et al. 2001; [f] Fleischer et al. 1994; [g] Petren et al. 1999; [i] Stutchbury et al. 1998; [j] Carvalho et al. 2006.

Many variables can affect extra-pair effort in breeding birds, but we have long argued that breeding synchrony is an important predictor of extra-pair mating systems at the species level (Stutchbury and Morton 1995, Morton et al. 1998, Stutchbury 1998). The frequency of EPFs is closely correlated with breeding synchrony among New World passerines (Stutchbury 1998, Stutchbury et al. 2005b) and is an important predictor of extra-pair mating systems in more general comparative analyses (Møller and Ninni 1998). We predicted that extra-pair mating systems would not be the norm because most tropical passerines are paired and territorial year round, and have long asynchronous breeding seasons. Due to the scarcity of paternity studies, our first evidence for low EPFs in tropical passerines came from their low testes size (Stutchbury and Morton 1995) and then from a handful of tropical passerines that were found to have few or no EPFs (Stutchbury and Morton 2001).

Given that mating systems may so thoroughly affect a species' biology, it is disconcerting that only three studies on tropical passerines have been published in the last 5 years, adding only four species to the tropical list (Gill et al. 2005, Carvalho et al. 2006, Stutch-

bury et al. 2007). To be fair, this is partly due to the logistical challenges of obtaining a decent sample size when faced with small brood sizes and high nest predation. There are now 10 species of tropical passerines, all from the Neotropics, where paternity data are available (Table 1). Half have fewer than 5% extra-pair young, and can be considered genetically monogamous.

Tropical species with relatively high synchrony, like the Lesser Elaenia (*Elaenia chiriquensis*), Clay-colored Thrush, and Blue-black Grassquit (*Volatinia jacarina*), have abundant EPFs (Stutchbury et al. 1998, 2007; Carvalho et al. 2006). Blue-black Grassquits are sexually dimorphic granivores that have high breeding synchrony due to rapid and synchronous maturation of grass seed crops in the rainy season. Males have a distinctive jump display from the grass accompanied by a complicated, but short, buzzy song. Females seem to prefer to mate with males having the highest jumps and this highly synchronized breeding is coupled with an extra-pair mating system (Carvalho et al. 2006).

Studies of closely related species that differ in breeding synchrony offer a more powerful test of the tie between synchrony and extra-pair behavior. One study compared EPF frequency in two *Elaenia* flycatchers that differ in breeding synchrony (Stutchbury et al. 2007). The Lesser Elaenia and the Yellow-bellied Elaenia (*Elaenia flavogaster*) breed during the dry season but the former is migratory and more synchronous whereas the latter is permanently paired and defends territories throughout the year. Both species are monogamously paired, share the same habitat, and have a fruit-influenced territorial system (Stutchbury and Morton 2001), but the Lesser Elaenia had a high level of extra-pair fertilizations (67% of broods, 37% of nestlings) while we detected only a single instance of extra-pair paternity in the Yellow-bellied Elaenia (8% of broods, 4% of nestlings). We hope the common occurrence of near-genetic monogamy in tropical passerines, and the intriguing differences among species documented thus far, will spur others to incorporate paternity analyses into their studies.

Testosterone and Mating System.—We suggested that testosterone appeared to relate more to achieving success in extra-pair mating than as a normal and necessary component of breeding behavior, which explains why temperate species have such high levels of testosterone compared with tropical passerines (Stutchbury and Morton 2001). Testosterone functions to maintain the exhausting aggression and displays that are associated with strong sexual selection and mate choice common to extra-pair mating systems (Raouf et al. 1997). Tropical species that do breed synchronously and have extra-pair matings are expected to have high testosterone levels, which is the case for the Clay-colored Thrush (1.8 ng ml^{-1}) (Wikelski et al. 2003a). Testosterone is also important in lekking species, like the Golden-collared Manakin (*Manacus vitellinus*), where testosterone increases display behavior (Day et al. 2006).

Testosterone has recently been tied specifically to extra-pair mating systems in temperate zone passerines (reviewed in Garamszegi et al. 2005). The model that best explains levels of testosterone suggests a primary relationship between relative testis size and extra-pair fertilizations with a secondary consequence on levels of testosterone (Garamszegi et al. 2005). An extra-pair mating system causes higher levels of testosterone, presumably because testosterone enhances behavior involved in the relative success of extra-pair fertilizations. Goymann et al. (2004) confirmed that average levels of testosterone were higher in northern temperate species than tropical species (2.8 ± 0.4 vs. 1.3 ± 0.2 ng ml^{-1}, $P < 0.0002$). They also showed that birds with short breeding seasons, including high altitude breeders, had high testosterone relative to those with long breeding seasons. Seasonally-breeding tropical birds with breeding season territoriality like temperate birds, had >2.0 ng ml^{-1} testosterone whereas birds with year-round territories had <1.0 ng ml^{-1}. They concluded that high testosterone can evolve in the tropics under conditions of short breeding seasons and high altitudes (Goymann et al. 2004). Short breeding seasons are associated with higher breeding synchrony and more intense pressure to establish a territory and find a mate. Short breeding seasons also appear to be associated with extra-pair mating systems in tropical birds (Table 1) which clearly would generate intense male-male competition. Analysis of testosterone relative

to type of territoriality and mating system was hampered by low statistical power—we don't know enough about tropical birds!

Whether the mating systems of lowland breeders or the high cost of lowered immunocompetence explains the evolution of low testosterone requires studies that uncouple the two variables. Many species in the lowland are seasonal breeders and have extra-pair mating systems, and presumably there are also high altitude breeders with relatively long breeding seasons. Comparisons of testosterone function in congeneric tropical birds that share the same habitat but differ in mating system, for instance the Elaenia example (Stutchbury et al. 2007) would be a powerful way to control for exposure to parasites and explore the role of testosterone in territory defense and immune function.

Territoriality and Song.—High adult survival is expected to result in relatively low turnover of territories, which could constrain opportunities for territory and mate switching by adults, as well as territory and mate choice by juveniles (Morton et al. 2000). In Dusky Antbirds (*Cercomacra tyrannina*), experimentally created vacancies are filled rapidly (<24 hrs), usually by neighboring territory holders (Morton et al. 2000). Both males and females of several species will quickly divorce their mates to fill vacant territories, likely to obtain a higher quality territory. Other species in similar habitat and the same study area in central Panama show a pattern of voluntary mate fidelity. In White-bellied Antbirds, for instance, experimentally-created vacancies were filled slowly (2–3 days) or not at all, and divorce was uncommon (Fedy and Stutchbury 2004).

Annual survival of territory holders in Buff-breasted Wrens (*Thryothorus leucotis*) is 68% for females and 76% for males. Natural vacancies occur regularly and are filled rapidly (<24 hrs), but in this species divorce did not occur between pairs which already bred together (Gill and Stutchbury 2006). A widowed bird is conspicuous to neighbors because it sings only it's half of the duet and one can presume that neighbors are aware of vacancies but choose not to move. Once a pair breeds together they remain paired until one member dies, so "til death do us part" actually applies. In contrast, divorce was relatively common in young birds that had been paired <5 months and had not yet bred together. The interesting twist is the propensity for divorce only applied to young birds that immigrated into the population. Juveniles which lived on their parent's territory before acquiring a territory nearby (1–2 territories away) generally did not divorce once paired, even when there were opportunities to switch territories. This suggests that local recruits can successfully assess territory and mate quality prior to acquiring a territory, whereas outsiders fill a vacancy first and then begin to assess other opportunities on neighboring territories. We do not yet know why mate fidelity is so advantageous for experienced pairs.

Male and female Dusky Antbirds exhibit sex-specific territory defense (Morton and Derrickson 1996). Male song playbacks elicit a stronger response from the male than the female (Bard et al. 2002), whereas female residents are more aggressive than their mates in response to female song playback. A recent study of another antbird, the Warbling Antbird (*Hypocnemis cantator*) went much further by showing that females sang more and more quickly, thus initiating more duets, when responding to female solo playbacks than to duet or male solo playbacks (Seddon and Tobias 2006). This supports the idea that duets are in defense of the mate rather than a form of cooperation in joint defense of the territory. Male White-bellied Antbirds responded more aggressively than females regardless of whether the stimulus was male song, female song, or duetting (Fedy and Stutchbury 2005). Both genders were more aggressive to playbacks during the non-breeding (dry) season than the breeding (wet) season, perhaps because the low arthropod abundance during the dry season increases the benefits of exclusive use of the territory. Duetting did not appear to function in territory defense since pairs did not duet more during playbacks, even when duet songs were used as a stimulus.

A typical White-bellied Antbird pair sang only several (1–3) duets/hr, <10 male songs/hr, and <3 female songs/hr (Fedy and Stutchbury 2005). There was no dawn chorus (e.g., elevated song rate) during the dry or wet season. In contrast, the Chestnut-backed Antbird (*Myrmeciza exsul*) has a dawn chorus (Stutchbury et al. 2005b). Possibly, the acoustic dif-

ferences between scrubby edge (White-bellied habitat) and shaded forest (Chestnut-backed habitat), in combination with habitat differences in food availability, have influenced the tendency to sing at dawn (Morton 1977, Seddon 2005).

Antbirds do not learn songs and their duets are simple relative to the elaborate repertoires of duets found in song-learning oscine passerines (Seddon and Tobias 2006). Perhaps the best example of how complex dueting can become is found in the Plain-tailed Wren (*Thryothorus euophrys*) where groups of birds sing in synchronized choruses, coordinating their repertoires of 20 phrases of sex-specific songs for up to 2 min (Mann et al. 2007)! Buff-breasted Wrens have a conspicuous dawn chorus following daybreak, when pairs typically sing over 50 duets in 30 min, often switching to different duet combinations (Gill et al. 2005).

The role of duet singing in territorial defense has taken on new significance with the discovery of a "duet code" in Black-bellied Wrens (*Thryothorus fasciatoventris*) (Logue and Gammon 2004, Logue 2006). As in most dueting bird species, males and females differ in their responses to intra- and inter-sexual playbacks with greater responses to same-sex songs. Female Black-bellied Wrens respond more to female songs but males do not differentiate to the same extent. However, the song contributions by pair members to each duet are not random. For each pair there exists a specific pairing of songs which is somewhat reciprocal. For example, if a male sings song A, his mate duets with her song W, and if her song W is played back, her mate responds with his song A. These couplings between songs in each duet constitute the duet code in this species and serve to identify specific individuals, useful information in defending territories. Rufous-and-white Wrens (*Thryothorus rufalbus*) sing mainly solo songs with males singing much more than females and males only singing in a dawn chorus. Playback experiments using stereo speakers imitating an intruding pair showed that Rufous-and-white Wrens also have a duet code that functions in territorial defense (Mennill and Vehrencamp 2005, Mennill 2006).

There are exciting new aspects of neotropical avian biology that have developed in the last 5 years with the traditional focus on passerine birds (Stutchbury and Morton 2001). The use of the diversity of tropical birds to evaluate and test ideas about general avian adaptations is still a largely untapped resource. We hope this mini-review encourages others to step outside the temperate zone bias and into the field to study tropical birds.

ACKNOWLEDGMENTS

We thank the Wilson Ornithological Society for awarding us the 2005 Margaret Morse Nice Medal. It is a great honor. We dedicate this review to the naturalists that Margaret Morse Nice, Alexander Skutch, and Eugene Eisenmann, among many others, mentored and hope the tradition of "knowing your organism" will increase as a way to enhance our scientific understanding of birds.

LITERATURE CITED

AHUMADA, J. A. 2001. Comparison of the reproductive biology of two neotropical wrens in an unpredictable environment in northeastern Colombia. Auk 118:191–210.

BALTHAZART, J. 1983. Hormonal correlates of behavior. Pages 221–365 *in* Avian biology. VII (D. S. Farner, J. R. King, and K. C. Parkes, Editors). Academic Press, New York, USA.

BARD, S. C., M. HAU, M. WIKELSKI, AND J. C. WINGFIELD. 2002. Vocal distinctiveness and response to conspecific playback in the Spotted Antbird, a neotropical suboscine. Condor 104:387–394.

CARVALHO, C. B. V., R. H. MACEDO, AND J. A. GRAVES. 2006. Breeding strategies of a socially monogamous neotropical passerine: extra-pair fertilizations, behavior, and morphology. Condor 108: 579–590.

DAY, L. B., J. T. MCBROOM, AND B. A. SCHLINGER. 2006. Testosterone increases display behaviors but does not stimulate growth of adult plumage in male Golden-collared Manakins (*Manacus vitellinus*). Hormones and Behavior 49:223–232.

DITTAMI, J. P. AND E. GWINNER. 1985. Annual cycles in the African Stonechat *Saxicola torquata axillaris* and their relationship to environmental factors. Journal of Zoology 207:357–370.

DURRANT, K. L., J. S. BEADELL, F. ISHIAQ, G. R. GRAVES, S. L. OLSON, E. GERING, M. A. PEIRCE, C. M. MILENSKY, B. K. SCHMIDT, C. GEBHARD, AND R. C. FLEISCHER. 2006. Avian hematozoa in South America: a comparison of temperate and tropical zones. Ornithological Monographs 60:98–111.

FEDY, B. C. AND B. J. M. STUTCHBURY. 2004. Territory switching and floating in a resident tropical passerine, the White-bellied Antbird. Auk 121:486–496.

FEDY, B. C. AND B. J. M. STUTCHBURY. 2005. Territory defence in tropical birds: are females as aggres-

sive as males? Behavioural Ecology and Sociobiology 58:414–422.

Fedy, B. C. and B. J. M. Stutchbury. 2006. Testosterone does not increase in response to conspecific challenges in the White-bellied Antbird (*Myrmeciza longipes*), a resident tropical passerine. Auk 123:61–66.

Ferreti, V., P. E. Llambías, and T. E. Martin. 2005. Life-history variation of a neotropical thrush challenges food limitation theory. Proceedings of the Royal Society of London B 272:769–773.

Fleischer, R. C., C. Tarr, and T. K. Pratt. 1994. Genetic structure and mating system in the Palila, an endangered Hawaiian honeycreeper, as assessed by DNA fingerprinting. Molecular Ecology 3:383–392.

Fleischer, R. C., C. L. Tarr, E. S. Morton, A. Sangmeister, and K. C. Derrickson. 1997. Mating system of the Dusky Antbird, a tropical passerine, as assessed by DNA fingerprinting. Condor 99: 512–514.

Folstad, I. and A. J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. American Naturalist 139:603–622.

Freed, L., J. S. Fretz, and M. C. Medeiros. 2007. Adaptation in the Hawaiian Akepa to breed and moult during a seasonal food decline. Evolutionary Ecology 9:157–167.

Garamszegi, L. Z., M. Eens, S. Hurtrez-Bousses, and A. P. Møller. 2005. Testosterone, testes size, and mating success in birds: a comparative study. Hormones and Behavior 47:389–409.

Ghalambor, C. K. and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494–497.

Gill, S. A. and B. J. M. Stutchbury. 2006. Long-term mate and territory fidelity in neotropical Buff-breasted Wrens (*Thryothorus leucotis*). Behavioral Ecology and Sociobiology 61:245–253.

Gill, S. A., M. J. Vonhof, B. J. M. Stutchbury, E. S. Morton, and J. S. Quinn. 2005. No evidence for acoustic mate-guarding in duetting Buff-breasted Wrens (*Thryothorus leucotis*). Behavioral Ecology and Sociobiology 57:557–565.

Goymann, W., I. T. Moore, A. Scheuerlein, K. Hirschenhauser, A. Grafen, and J. C. Wingfield. 2004. Testosterone in tropical birds: effects of environmental and social factors. American Naturalist 164:327–334.

Goymann, W., D. Geue, I. Schwabl, H. Flinks, D. Schmidl, H. Schwabl, and E. Gwinner. 2006. Testosterone and corticosterone during the breeding cycle of equatorial and European Stonechats (*Saxicola torquata axillaris* and *S. t. rubicola*). Hormones and Behavior 50:779–785.

Greenman, C. G., L. B. Martin II, and M. Hau. 2005. Reproductive state, but not testosterone, reduces immune function in male House Sparrows (*Passer domesticus*). Physiological and Biochemical Zoology 78:60–68.

Hau, M. 2001. Timing of breeding in variable environments: tropical birds as model systems. Hormones and Behavior 40:281–290.

Hau, M. 2007. Regulation of male traits by testosterone: implications for the evolution of vertebrate life histories. BioEssays 29:133–144.

Hau, M., M. Wikelski, K. K. Soma, and J. C. Wingfield. 2000. Testosterone and year-round territorial aggression in a tropical bird. General and Comparative Endocrinology 117:20–33.

Helm, B., E. Gwinner, and L. Trost. 2005. Flexible seasonal timing and migratory - behavior results from Stonechat breeding programs, Pages 216–227 *in* Bird hormones and bird migrations: analyzing hormones in droppings and egg yolks and assessing adaptations in long-distance migration. (W. Goymann, S. Jenni-Eirmann, and U. Bauchinger, Editors). Annals of the New York Academy of Sciences, Blackwell Publishing, New York, USA.

Hillgarth, N. and J. C. Wingfield. 1997. Parasite-mediated sexual selection: endocrine aspects. Pages 78–104 *in* Host-parasite evolution: general principles and avian models (D. H. Clayton and J. Moore, Editors). Oxford University Press, Oxford, United Kingdom.

Hirschenhauser, K., H. Winkler, and R. F. Oliveira. 2003. Comparative analysis of male androgen responsiveness to social environment in birds: the effects of mating system and paternal incubation. Hormones and Behavior 43:508–519.

Kempenaers, B. 1993. The use of a breeding synchrony index. Ornis Scandinavica 24:84.

Ketterson, E. D., V. Nolan Jr., and M. Sandell. 2005. Testosterone in females: mediator of adaptive traits, constraint on sexual dimorphism, or both? American Naturalist 166:S85–S98.

Levin, R. N. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. 1. Removal experiments. Animal Behaviour 52:1093–1106.

Levin, R. N. and J. C. Wingfield. 1992. The hormonal control of territorial aggression in tropical birds. Ornis Scandinavica 23:284–291.

Logue, D. M. 2006. The duet code of the female Black-bellied Wren. Condor 108:326–335.

Logue, D. M. and D. E. Gammon. 2004. Duet song and sex roles during territory defence in a tropical bird, the Black-bellied Wren, *Thryothorus fasciatoventris*. Animal Behaviour 68:721–731.

Mann, N. I., K. A. Dingess, and P. J. B. Slater. 2006. Antiphonal four-part synchronized chorusing in a neotropical wren. Biology Letters 2:1–4.

Martin, T. E., A. P. Møller, S. Merino, and J. Clobert. 2001. Does clutch size evolve in response to parasites and immunocompetence? Proceedings of the National Academy of Sciences 98:2071–2076.

Martin II, L. B., D. Hasselquist, and M. Wikelski. 2006. Investment in immune defense is linked to pace of life in House Sparrows. Oecologia 147: 565–575.

Mennill, D. J. 2006. Aggressive responses of male

and female Rufous-and-white Wrens to stereo duet playback. Animal Behaviour 71:219–226.

MENNILL, D. J. AND S. L. VEHRENCAMP. 2005. Sex differences in singing and duetting behavior of neotropical Rufous-and-white Wrens (*Thryothorus rufalbus*). Auk 122:175–186.

MØLLER, A. P. AND P. NINNI. 1998. Sperm competition and sexual selection: a meta-analysis of paternity studies in birds. Behavioral Ecology and Sociobiology 43:345–358.

MOORE, I. T., B. G. WALKER, AND J. C. WINGFIELD. 2004b. The effects of combined aromatase inhibitor and anti-androgen on male territorial aggression in a tropical population of Rufous-collared Sparrows, *Zonotrichia capensis*. General and Comparative Endocrinology 135:223–229.

MOORE, I. T., N. PERFITO, H. WADA, T. S. SPERRY, AND J. C. WINGFIELD. 2002. Latitudinal variation in plasma testosterone levels in birds of the genus *Zonotrichia*. General and Comparative Endocrinology 129:13–19.

MOORE, I. T., H. WADA, N. PERFITO, D. S. BUCH, T. P. HAHN, AND J. C. WINGFIELD. 2004a. Territoriality and testosterone in an equatorial population of Rufous-collared Sparrows, *Zonotrichia capensis*. Animal Behaviour 67:411–420.

MOORE, O. R., B. J. M. STUTCHBURY, AND J. S. QUINN. 1999. Extrapair mating system of an asynchronously breeding tropical songbird: the Mangrove Swallow. Auk 116:1039–1046.

MORTON, E. S. 1971. Nest predation affecting the breeding season of the Clay-colored Robin, a tropical song bird. Science 181:920–921.

MORTON, E. S. 1977. On the occurrence and significance of motivational-structural rules in some bird and mammal sounds. American Naturalist 111: 855–869.

MORTON, E. S. 1996. A comparison of vocal behavior among tropical and temperate passerine birds. Pages 258–268 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and T. E. Miller, Editors). Cornell University Press, Ithaca, New York.

MORTON, E. S. AND K. C. DERRICKSON. 1996. Song ranging by the Dusky Antbird, *Cercomacra tyrannina*: song ranging without learning. Behavioral Ecology and Sociobiology 39:195–201.

MORTON, E. S., B. J. M. STUTCHBURY, AND K. C. DERRICKSON. 2000. Territory switching behavior in a sedentary tropical passerine, the Dusky Antbird *Cercomacra tyrannina*. Behavioral Ecology 11: 648–653.

MORTON, E. S., B. J. M. STUTCHBURY, AND W. PIPER. 1998. Genetic monogamy in Blue-headed Vireos, and a comparison with a sympatric vireo with extrapair paternity. Behavioral Ecology 9:515–524.

MORTON, M. L., L. E. PETERSON, D. M. BURNS, AND N. ALLAN. 1990. Seasonal and age-related changes in plasma testosterone levels in mountain White-crowned Sparrows. Condor 92:166–173.

PEACH, W. J., D. B. HANMER, AND T. B. OATLEY. 2001. Do southern African songbirds live longer than their European counterparts? Oikos 93:235–249.

PETREN, K., B. R. GRANT, AND P. R. GRANT. 1999. Low extrapair paternity in the Cactus Finch (*Geospiza scandens*). Auk 116:252–256.

RICKLEFS, R. E. 1992. Embryonic development period and the prevalence of avian blood parasites. Proceedings of the National Academy of Sciences of the United States of America 89:4722–4725.

RICKLEFS, R. E. AND M. WIKELSKI. 2002. The physiology/life-history nexus. Trends in Ecology and Evolution 17:462–468.

RAOUF, S. A., P. G. PARKER, E. D. KETTERSON, V. NOLAN JR., AND C. ZIEGENFUS. 1997. Testosterone influences reproductive success by increasing extrapair fertilizations in male Dark-eyed Juncos, *Junco hyemalis*. Proceedings of the Royal Society of London, Series B, 264:1599–1603.

ROBERTS, M. L., K. L. BUCHANAN, AND M. R. EVANS. 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. Animal Beahviour 68:227–239.

ROBERTSON, B. C., S. M. DEGNAN, J. KIKKAWA, AND C. C. MORITZ. 2001. Genetic monogamy in the absence of paternity guards: the Capricorn Silvereye, *Zosterops lateralis chlorocephalus*, on Heron Island. Behavioral Ecology 12:666–673.

RODL, T., W. GOYMANN, I. SCHWABL, AND E. GWINNER. 2004. Excremental androgen metabolite concentrations and gonad sizes in temperate zone vs. tropical Stonechats (*Saxicola torquata* ssp.). General and Comparative Endocrinology 139:124–130.

RUSSELL, E. M., Y. YOM-TOV, AND E. GEFFEN. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behavioral Ecology 15:831–838.

SCHWABL, H., H. FLINKS, AND E. GWINNER. 2005. Testosterone, reproductive stage, and territorial behavior of male and female European Stonechats *Saxicola torquata*. Hormones and Behavior 47: 503–512.

SEDDON, N. 2005. Ecological adaptation and species recognition drives vocal evolution in noetropical suboscine birds. Evolution 59:200–215.

SEDDON, N. AND J. A. TOBIAS. 2006. Duets defend mates in a suboscine passerine, the Warbling Antbird (*Hypocnemis cantator*). Behavioral Ecology 17:73–83.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

SKUTCH, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Pages 575–594 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Editors). Volume 36. American Ornithologists' Union, Washington, D.C., USA.

STUTCHBURY, B. J. M. 1998. Female mate choice of extra-pair males: breeding synchrony is important.

Behavioural Ecology and Sociobiology 43:213–215.

Stutchbury, B. J. and E. S. Morton. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. Behaviour 132:675–690.

Stutchbury, B. J. M. and E. S. Morton. 2001. Behavioral ecology of tropical birds. Academic Press, London, United Kingdom.

Stutchbury, B. J. M., E. S. Morton, and W. H. Piper. 1998. Extra-pair mating system of a synchronously breeding tropical songbird. Journal of Avian Biology 29:72–78.

Stutchbury, B. J. M., E. S. Morton, and T. E. Pitcher. 2005a. Sex roles in migrants: extra-pair mating systems and winter social systems. Pages 307–320 *in* Birds of two worlds: the ecology and evolution of migratory birds (R. Greenberg and P. Marra, Editors). Johns Hopkins University Press, Baltimore, Maryland, USA.

Stutchbury, B. J. M., E. S. Morton, and B. Woolfenden. 2007. Comparison of the mating systems and breeding behavior of a resident and a migratory tropical flycatcher. Journal of Field Ornithology 78:40–49.

Stutchbury, B. J. M., B. E. Woolfenden, B. C. Fedy, and E. S. Morton. 2005b. Nonbreeding territorial behaviour of two congeneric antbirds, *Myrmeciza exsul* and *M. longipes*. Ornithologia Neoptropical 16:397–404.

Styrsky, J. N., J. D. Brawn, and S. K. Robinson. 2005. Juvenile mortality increases with clutch size in a neotropical bird. Ecology 86:3238–3244.

Tieleman, B. I., J. B. Williams, R. E. Ricklefs, and K. C. Klasing. 2005. Constitutive innate immunity is a component of the pace-of-life syndrome in tropical birds. Proceedings of the Royal Society of London Series B-Biological Sciences 272: 1715–1720.

Tieleman, B. I., T. H. Dijkstra, J. R. Lasky, R. A. Mauck, G. H. Visser, and J. B. Williams. 2006. Physiological and behavioural correlates of life-history variation: a comparison between tropical and temperate zone House Wrens. Functional Ecology 20:491–499.

Wada, H., I. T. Moore, C. W. Breuner, and J. C. Wingfield. 2006. Stress responses in tropical sparrows: comparing tropical and temperate *Zonotrichia*. Physiological and Biochemical Zoology 79:784–792.

Weathers, W. W. 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. Auk 114:341–353.

Wikelski, M., M. Hau, and J. C. Wingfield. 1999. Social instability increases plasma testosterone in a year-round territorial neotropical bird. Proceedings of the Royal Society of London Series B, Biological Sciences 266:551–556.

Wikelski, M., M. Hau, W. D. Robinson, and J. C. Wingfield. 2003a. Reproductive seasonality of seven neotropical passerine species. Condor 105: 683–695.

Wikelski, M., L. Spinney, W. Schelsky, A. Scheuerlein, and E. Gwinner. 2003b. Slow pace of life in tropical sedentary birds: a common-garden experiment on four Stonechat populations from different latitudes. Proceedings of the Royal Society of London Series B, Biological Sciences 270: 2383–2388.

Wiley, C. J. and A. W. Goldizen. 2003. Testosterone is correlated with courtship but not aggression in the tropical Buff-banded Rail, *Gallirallus philippensis*. Hormones and Behavior 43:554–560.

Wingfield, J. C. and T. P. Hahn. 1994. Testosterone and territorial behaviour in sedentary and migratory sparrows. Animal Behaviour 47:77–89.

Wingfield, J. C., S. E. Lynn, and K. K. Soma. 2001. Avoiding the 'costs' of testosterone: ecological bases of hormone-behavior interactions. Brain Behavior and Evolution 57:239–251.

Wingfield, J. C., R. E. Hegner, J. A. Dufty, and G. F. Ball. 1990. The "Challenge hypothesis": theoretical implications for pattern of testosterone secretion, mating systems, and breeding strategies. American Naturalist 136:829–846.

The Wilson Journal of Ornithology 120(1):38–49, 2008

DISTRIBUTION, BEHAVIOR, AND CONSERVATION STATUS OF THE RUFOUS TWISTWING (*CNIPODECTES SUPERRUFUS*)

JOSEPH A. TOBIAS,[1,7] DANIEL J. LEBBIN,[2] ALEXANDRE ALEIXO,[3] MICHAEL J. ANDERSEN,[4] EDSON GUILHERME,[5] PETER A. HOSNER,[6] AND NATHALIE SEDDON[1]

ABSTRACT.—The Rufous Twistwing (*Cnipodectes superrufus*), a newly described Amazonian tyrant-flycatcher, is known from five specimens and five localities in Cuzco and western Madre de Dios departments, Peru. We report three additional specimens and eight new localities extending the known range of the species east across Dpto. Madre de Dios, Peru, into Dpto. Pando, Bolivia, and Acre State, Brazil. The new localities increase the distribution from ~3,400 to ~89,000 km^2. We collected biometric data from five individuals, made behavioral observations in the field, and recorded three separate types of vocalizations, two of which (including the song) were previously unknown. We provide quantitative description of these vocalizations, consider their function, and compare them with vocalizations of the only known congener, the Brownish Twistwing (*Cnipodectes subbrunneus*). Unique vocal repertoires support the classification of these two forms as sister species. The Rufous Twistwing resembles the Brownish Twistwing in producing loud vocalizations from regular song posts and both species appear to have a polygamous mating system. We provide further evidence consistent with the hypothesis the Rufous Twistwing is a *Guadua* bamboo specialist and recommend that it be listed as Vulnerable on the IUCN Red List. *Received 5 July 2006. Accepted 23 March 2007.*

The Rufous Twistwing (*Cnipodectes superrufus*) is a large, distinctive tyrant-flycatcher from southwest Amazonia. It occurs in a region relatively well studied by ornithologists, but was only recently described and little is known about its behavior, distribution, and population size (Lane et al. 2007).

The only previous publication considered the Rufous Twistwing likely to be a *Guadua* bamboo specialist, but noted that it was almost certainly heard in "river-edge thicket vegetation with no bamboo growth visible" at Manu Lodge (12° 06′ S, 71° 06′ W; elevation 340 m) in 1991 and 2000 (Lane et al. 2007: 768). The five confirmed localities (Lane et al. 2007) encompass a small area (~3,400 km^2) in western Dpto. Madre de Dios and Dpto. Cuzco, Peru. However, the existence of large blocks of *Guadua* bamboo-dominated *terra firme* forest in southwestern Amazonian Brazil, southeastern Peru, and northwestern Bolivia (Silman et al. 2003) suggest the global distribution of the species may be extensive (Lane et al. 2007).

The only published vocalization is an agitation call (Lane et al. 2007), whereas the full vocal repertoire is likely to be similar to that of the Brownish Twistwing (*C. subbrunneus*), a presumed sister species with at least three distinct vocalizations (Parker and Remsen 1987, Schulenberg et al. 2000, Ridgely and Greenfield 2001). Male Brownish Twistwings are notably disinterested in playbacks of their songs, which are given from small, stable, and often adjacent territories, suggesting a polygynous mating system (Parker and Remsen 1987, Ridgely and Tudor 1994, Ridgely and Greenfield 2001, Fitzpatrick 2004). Lane et al. (2007) reported no information regarding the breeding behavior of Rufous Twistwing.

In this paper we report: (1) new localities, (2) vocalizations, (3) habitat preferences, and (4) behavior of the Rufous Twistwing to add to the details presented by Lane et al. (2007). We also assess the conservation status of the species, based on our results, following IUCN Red List criteria (IUCN 2001).

[1] Edward Grey Institute, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, United Kingdom.

[2] Department of Ecology and Evolutionary Biology, Cornell University, E148 Corson Hall, Ithaca, NY 14853, USA.

[3] Museu Paraense Emílio Goeldi, Coordenação de Zoologia, Caixa Postal 399, 66040-170, Belém PA, Brazil.

[4] Macaulay Library, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.

[5] Universidade Federal do Acre, Departmento de Ciências da Natureza, BR-364, km 04, Campus, 69915-900, Rio Branco AC, Brazil.

[6] Cornell Museum of Vertebrates, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.

[7] Corresponding author;
e-mail: joseph.tobias@zoo.ox.ac.uk

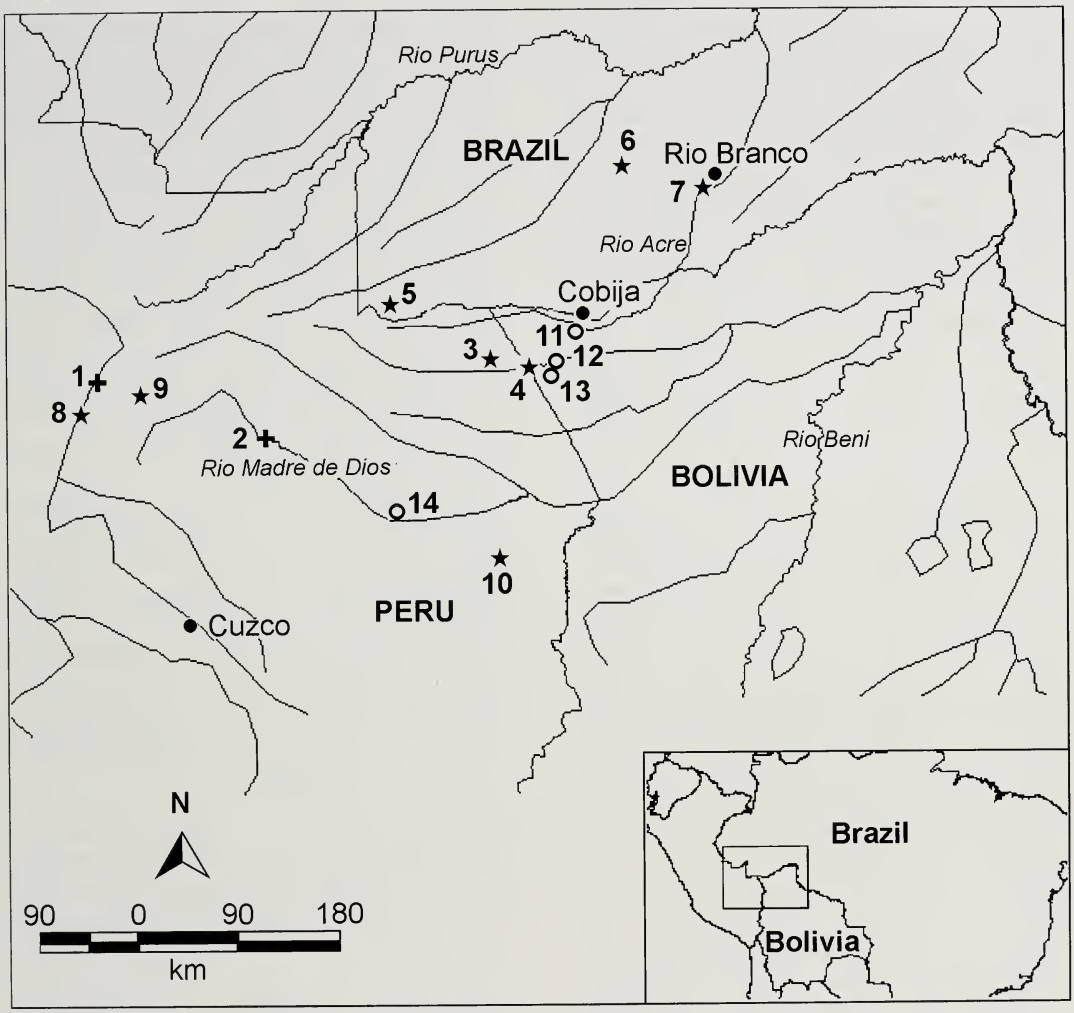


FIG. 1. Sites mentioned in the text mapped in relation to major cities (closed circles), rivers, and international boundaries. Crosses indicate the previously known range of Rufous Twistwing in Peru: (1) Río Urubamba centered on Camisea, and (2) Río Manu centered on Pakitza, Dpto. Madre de Dios (type locality). Stars indicate new localities for the species: (3) Oceanía, Dpto. Madre de Dios, Peru; (4) Extrema, Dpto. Pando, Bolivia; (5) Estação Ecológica do Rio Acre, Acre State, Brazil; (6) Ramal Jarinal, Acre State, Brazil; (7) Rio Branco, Acre State, Brazil; (8) Timpía, Dpto. Cuzco, Peru; (9) Montetoni, Dpto. Cuzco, Peru; and (10) Tambopata, Dpto. Madre de Dios, Peru. Open circles indicate study sites where *C. superrufus* was absent: (11) Camino Mucden, Dpto. Pando, Bolivia; (12) Palmera, Dpto. Pando, Bolivia; (13) San Sebastián, Dpto. Pando, Bolivia; and (14) CICRA, Dpto. Madre de Dios, Peru.

METHODS

Study Sites and Survey Methods.—We surveyed six *Guadua*-dominated forest sites in southwestern Amazonia, including one site in Bolivia and three in Brazil. Avifaunal surveys were undertaken by three independent teams at field sites using different methods at each site except CICRA and Oceanía where the same methods were used. Playback of pre-recorded Rufous Twistwing calls was used opportunistically at sites 1–3; in all cases we used the agitated calls recorded by Thomas Valqui H. at Kirigueti, Dpto. Cuzco, (i.e., Fig. 3A in Lane et al. 2007). Additional records were sought from experienced observers. Localities were mapped (Fig. 1) and range sizes measured using equal-area projections with ArcView 3.2.

1. Centro de Investigación y Capacitación Río Los Amigos (CICRA), 270 m, Dpto. Madre de Dios, Peru (12° 35′ S, 69° 12′ W), 2001–2007. This research station is at the confluence of the Río Los Amigos and the Río Madre de Dios in the Los Amigos Conservation Concession, a 135,000-ha private concession managed by Amazon Conservation Association. DJL, MJA, PAH, JAT, and NS surveyed multiple patches of *Guadua weberbaueri* and *G. sarcocarpa* bamboo for multiple bird species over a 7-year period using random transects, field observations, tape-recording, and intensive mist netting. This site includes camp CM1 on the south bank of the Río Los Amigos.

2. Oceanía, 250 m, Dpto. Madre de Dios, Peru (11° 23′ S, 69° 32′ W), 11–18 October 2004. This locality is 6 km west of Iberia, a town ~130 km north of Puerto Maldonado on the Iñapari road. DJL, MJA, and PAH surveyed a large patch of *Guadua weberbaueri* and *G. sarcocarpa* bamboo, in places collapsing to form impenetrable thickets with a canopy at ~4 m. The bamboo patch was on an upland terrace, bordered by land recently cleared and burned for agriculture, extending to the nearby Río Tahuamanu (to the east and south), as well as successional forest and mature forest (to the north, south, and west). The presence of burned and chained logs, and a logging road revealed a recent history of human disturbance. We conducted daily censuses using random transects between 0445 and 1000 hrs EST (12–16 Oct), and operated mist nets daily from dawn until midday (11–17 Oct). A combination of 6- and 12-m nets were rotated over 30 net locations covering a total length of 700 m of trail in 7 days. Total effort was ~400 net hrs (for 12-m nets).

3. Extrema, 250 m, Dpto. Pando, Bolivia (11° 28′ S, 69° 15′ W), 6–9 November 2004. This military outpost is ~45 km east-southeast of the Oceanía site on the banks of the Río Tahuamanu where this river flows from Peru into Bolivia. The natural habitat appears to be forest with an open canopy and an understory largely composed of *Guadua* bamboo. JAT and NS surveyed habitat here and at the adjacent guard-post of Alto Peru, 1 km north in Dpto. Madre de Dios, Peru. We surveyed habitat with and without bamboo on random transects between 0445 and 1800 hrs daily (6–9 Nov), spending 18 hrs in bamboo at Extrema and 2 hrs in bamboo at Alto Peru, Madre de Dios, Peru (2 km from Extrema).

4. Estação Ecológica do Rio Acre, 250–350 m, Acre State, Brazil (11° 03′ S, 70° 12′ W) on the border with Peru, 13–24 August 2005 and 3–15 February 2006. Site A was surveyed in 2005 by AA, including riparian forest along Rio Acre and a small tributary (Igarapé do Tombo); AA and EG surveyed site B, ~7 km west of site A, in 2006. Extensive patches of *Guadua* bamboo were present at both sites. Field effort included ~250 hrs of random transects through the main vegetation types, observing, mist netting, tape-recording, and collecting birds.

5. Rio Branco, 250 m, Acre State, Brazil (09° 57′ S, 67° 57′ W), 1998–2006. Long-term fieldwork is being conducted by EG at Parque Zoobotânico, a field station managed by Universidade Federal do Acre. The site is within the suburban limits of Rio Branco and the habitat (~100 ha of humid forest with patches of *Guadua sarcocarpa* and *G. weberbaueri* bamboo) is becoming increasingly disturbed and isolated by peripheral clearance (Guilherme 2001). The main survey technique was mist netting: 10 mist nets (12 m) were operated for 6 hrs/day (usually dawn until midday) on ~35 days/year (evenly split between dry and wet seasons). Annual mist netting effort was ~2,000 net hrs.

6. Ramal Jarinal, 320 m, ~100 km WNW of Rio Branco, Acre State, Brazil (09° 54′ S, 68° 28.5′ W), 12–22 November 2006. EG and Marcos Pérsio D. Santos (Universidade Federal do Piauí) surveyed this site and collected specimens. The habitat was *terra firme* forest dominated by bamboo (*Guadua sarcocarpa* and *G. weberbaueri*) and palms (e.g., *Attalea* sp.) with high human disturbance including recently cleared cattle pastures and selective logging.

Sound Recording, Analysis, and Playback Experiments.—Recordings of vocalizations were made at Oceanía and Extrema using a Sennheiser ME 67 shotgun microphone with a Sony PCM-M1 MiniDAT or a Sony TC-D5 Pro II Cassette Recorder. All recordings are deposited at the Macaulay Library (ML) at Cornell University.

Recordings were automatically filtered and digitized at a sampling frequency of 44.1 kHz

using Avisoft SASLabPro Version 4.15 (© 2002 Raimund Specht, Berlin, Germany) with a 16-bit acquisition sound card (0 VIA [Wave] 5.10). Sonograms were generated using standard broadband (216 Hz) filter settings (FFT = 1,024, Frame = 75%, Window = FlatTop, Overlap = 87.5%). Sonograms were inspected visually, assigned to three types, and described quantitatively using on-screen cursors to measure standard temporal (sec) and frequency (kHz) parameters: overall duration, duration of first note, duration of middle note, duration of final note, number of notes, pace of notes (notes/min within a vocalization), pace of calls (calls/min within a recording), maximum overall frequency, minimum overall frequency, and bandwidth.

Playback experiments were conducted at Extrema to investigate the function of vocalizations. Recordings were played through a Sony SRS-58 speaker from a range of 10–40 m; the subject of most playbacks (7/10) was the individual from which the tape was recorded. Samples were too small to permit statistical analysis.

RESULTS

Field Observations.—Intensive field work at CICRA has not yet produced records of the Rufous Twistwing, despite extensive bamboo and a broad community of bamboo-specialist birds. The species was more readily found at other sites, including Oceanía, where it was encountered 19 times (1–4 times daily) during an 8-day survey. Fifteen of these encounters were aural and four were visual; two observations lasted <1 min, one lasted ~20 min, and one lasted ~45 min. At least three individuals were involved (2 were color-banded and 1 unbanded bird was later seen).

The first record for Bolivia involved at least four individuals at Extrema where the species was encountered on 11 occasions during a 4-day survey. Eight observations were aural and three were visual. Ten encounters were within 2 km of the Extrema guard-post and one encounter was within Peru near the Alto Peru guard-post. One bird was photographed and tape-recorded on 7 November 2004; at least three other individuals were heard or seen daily along a 2-km transect.

The first record for Brazil involved a single individual mist netted and photographed at Parque Zoobotânico, Rio Branco on 22 May 1998, although it was only identified to species in February 2006. The species was encountered repeatedly at Parque Zoobotânico from 1998 onwards: nine individuals were mist netted, one specimen was collected, and another window-killed individual was found and prepared as a specimen. Both specimens are currently housed at Museu Paraense Emílio Goeldi (MPEG), Belém, Brazil (Table 1).

The Rufous Twistwing was encountered at two further Brazilian sites. It was found once at Estação Ecológica do Rio Acre during ~250 hrs of field work: AA heard and tape-recorded a single individual on 15 August 2005 in the dense understory of an extensive thicket of *Guadua* bamboo along a narrow creek (Igarapé do Tombo). Another individual was found by EG and Marcos Pérsio D. Santos on 20 November 2006 at Ramal Jarinal and a male was heard calling consistently throughout the morning from a *Guadua* bamboo thicket in *terra firme* forest. It was attracted with playback of its own calls and was collected; the skin is stored in MPEG (Table 1).

Three other localities have recently come to light (Fig. 1). The Rufous Twistwing was found three times near the Machiguenga community of Timpía (12° 04′ S, 72° 49′ W; elevation 410 m) on the Río Urubamba, Dpto. Cuzco, in 1998–2001 (N. G. Gerhart, pers. comm.). It was also recorded once nearby at Río Shihuaniro, a tributary of the Río Timpía, in October 1998 and once near Montetoni (11° 54′ S, 72° 21′ W; elevation 550 m) on the upper Río Camisea, Dpto. Cuzco in April 1998 (N. G. Gerhart, pers. comm.). A retrospective report involves a single individual in *Guadua* bamboo at Explorer's Inn, Tambopata (13° 08′ S, 69° 36′ W; elevation 250 m) in March 1984 (Michael Kessler, pers. comm.). The Río Shihuaniro locality is documented with a sound recording (ML 125894), as are the Timpía and Montetoni localities (N. G. Gerhart, pers. comm.); the Tambopata record is supported by a convincing description by an experienced observer. Adding the eight new localities to the original five produces a global range of ~89,000 km² (Fig. 1).

Mist Netting and Specimen Data.—Two birds were mist netted at Oceanía on 12 October 2004, a capture rate of one bird per ~200 net hrs (for 12-m nets). Both birds had

TABLE 1. Measurements of Rufous Twistwings (n = 5).

Locality	Date	Age/Gender	Wing length (mm)[a]	Tail (mm)	Bill length (mm)[b]	Bill width (mm)[c]	Tarsus (mm)[d]	Mass (g)	Catalog number
Oceanía[e]	12 Oct 2004	Adult/Male	117	108	18.6	6.4	25.3	42	—
Oceanía[e]	12 Oct 2004	Subadult?/Male	114	111	17.2	6.1	21.9	42	—
Rio Branco[f]	01 Oct 2003	Subadult?/Female?	88.3	87	16.27	6.6	19.1	22	60001
Rio Branco[f]	25 Feb 2006	Subadult/Male	100.3	95.4	17.73	6.9	20.3	35	60000
Ramal Jarinal[f]	20 Nov 2006	Adult/Male	118.7	113.5	20.08	7.3	22.5	41	61351

[a] Flattened wing chord.
[b] Exposed culmen.
[c] Measured at mid-nares.
[d] Measured from tibiotarsus/tarsometatarsus joint to ventral base of halux.
[e] From live birds by PAH.
[f] From MPEG specimens by AA.

modified primaries suggesting they were males. One individual had 100% skull ossification and was molting secondaries, upper tail coverts, and extensively over the body; the other individual (possibly subadult) had roughly 50% skull ossification, shorter crest feathers, and no molt.

Two of nine birds mist netted at Rio Branco were banded with color bands (1998) and five with metal rings (2 in 1999, 1 in 2000, 1 in 2004, and 1 in 2005). Only one of these nine birds was recaptured (once) and only one bird was considered to be juvenile (in June) on the basis of downy underwing plumage and traces of a commisure. The trapping rate was ~one bird/1,800 net hrs (for 12-m nets). Unfortunately, no biometric data were collected from these mist net captures. An immature bird found dead at Rio Branco in October was undergoing molt of remiges, rectrices, and contour feathers. The male collected at Ramal Jarinal on 20 November 2006 was an adult with enlarged testes.

Biometric data for two mist-netted birds and three specimens varied (Table 1). Measurements at Oceanía were from live birds and cannot be compared directly with other biometrics as specimens tend to shrink slightly during drying. Our sample is consistent with earlier data as males were considerably larger than females in mass and wing-length, but more similar in terms of bill and tarsus size. Total length of three fresh specimens was 18.4–24 cm.

Habitat.—We report 44 encounters with the Rufous Twistwing (combining field observations with mist net data) of which 43 were in or immediately adjacent to patches of *Guadua* bamboo. It was recorded at Oceanía only within one large patch of *Guadua* bamboo. Eighteen of 19 encounters were in dense ~5-m tall bamboo and one was in taller, sparser bamboo under mature forest. It occurred at Extrema in large stands of *Guadua* bamboo, apparently preferring areas with a highly discontinuous tree canopy, occurring either in low treeless growth where the bamboo had collapsed (canopy height 2–4 m), or in taller bamboo supported by scattered trees (canopy height 10–25 m); two of 11 encounters were in the former habitat and seven in the latter habitat. The species was also heard and tape-recorded on two occasions at Extre-

ma in an extensive patch of young secondary forest with a dense understory (canopy height ~10–15 m). This habitat contained only small amounts of bamboo but bordered an extensive stand of *Guadua*. The record at Montetoni was in scrubby secondary forest with a broken canopy, a dense understory of vines, and patches of *Guadua* bamboo; two records at Timpía were in similar broken secondary forest with dense bamboo dominating the understory (N. G. Gerhart, pers. comm.). We failed to detect the species at all sites in forest types lacking bamboo, although one recent observation by N. G. Gerhart (pers. comm.) was in dense secondary forest near Timpía with no bamboo component.

The Rufous Twistwing appears to be restricted to the understory. Birds at Oceanía foraged 1–3 m above ground, usually at the lower end of that scale. Similarly, individuals watched at Extrema did not ascend higher than 3 m above ground and spent most of their time at 1–2 m.

Movement and Flight.—DJL and PAH observed one Rufous Twistwing continuously for 45 min at Oceanía as it performed 32 wing raises in the following sequence: RRRRRR LLLLLLR (R/L) LLRRRRRRRRRRLLLR LL (bracketed codes denote right and left wing simultaneous raises). The impression given during this bout, and throughout all other field observations, was a strong preference for single-wing raises, with both wings favored in roughly equal proportion. This individual made significantly more wing raises by raising the same wing repeatedly (23) than by switching between wings (7): $\chi^2 = 8.53$, $P = 0.003$ (ignoring the simultaneous raise). Wing raising did not seem to correlate with any particular context, usually occurring randomly during bouts of vocalizing and foraging. There was no discernable increase in rate for birds accompanied by a second individual or in response to playback of calls.

The flight action of the Rufous Twistwing when moving between perches through the understory was erratic with slightly floppy and irregular downbeats. It was seen flying low across roads on three occasions at Extrema, at which time its flight was stronger and more direct.

Foraging Behavior.—The Rufous Twistwing foraged for prey from fairly open, often horizontal perches, slowly rotating the head to search at different angles. Individuals perched with an upright posture and flew to a new perch after 30–300 sec. They made abrupt sallies to small branches or leaves (bamboo and non-bamboo) to snatch invertebrates. One individual at Oceanía made three direct, upward, 1-m sallies from a horizontal bamboo stem to glean prey from bamboo leaves. It flew after each strike to a new perch at the same level as the original perch (once), or to a lower perch (twice). Another individual performed at least two upward sallies, two downward sallies, and one horizontal sally towards prey on small bamboo branches and leaves during a 45-min period. In one typical sally the bird traveled ~30 cm upward, plucked a prey item from a dead bamboo branch (with dry leaves), and then dropped to a lower perch. It was observed in the same 45-min period beating one ~20-mm orthopteran against a branch. Other prey items taken were small, unidentifiable, and swallowed immediately.

Vocalizations.—We grouped all vocalizations into three categories from a total of ~150 min of recorded vocalizations. These categories may not encompass the species' entire repertoire, but it is likely they cover all regularly given vocalizations.

Vocalization #1 is a loud, non-stereotyped, scolding series. It was heard during 25 encounters at Oceanía and Extrema. The full call is a loud series of 2–14 notes each containing at least three, usually four, harmonics (Fig. 2A) and is, at times, preceded by one or two loud *pyew* calls (Vocalization #3). The phrase (without the *pyew* call) is fairly even in pitch and pace, and is usually repeated during prolonged bouts at a rate ($\bar{x} \pm$ SD) of 13.8 ± 8.9 calls/min (n = 30 calls, from 3 bouts of calling by 2 individuals; Table 2).

Vocalization #1 is deposited at the Macaulay Library, Cornell University (catalog numbers ML 124448, 124449, 124450). It was recorded at Oceanía and heard irregularly at Extrema. A similar call was also recorded at Extrema; it was more subdued with fewer notes per series (ML 124455, Fig. 3B). The loud version was heard throughout the day, often in late morning and mid-afternoon when most other species were silent; the quiet call was given at 1630 hrs on 6 November 2004. Both loud and quiet versions are similar in struc-

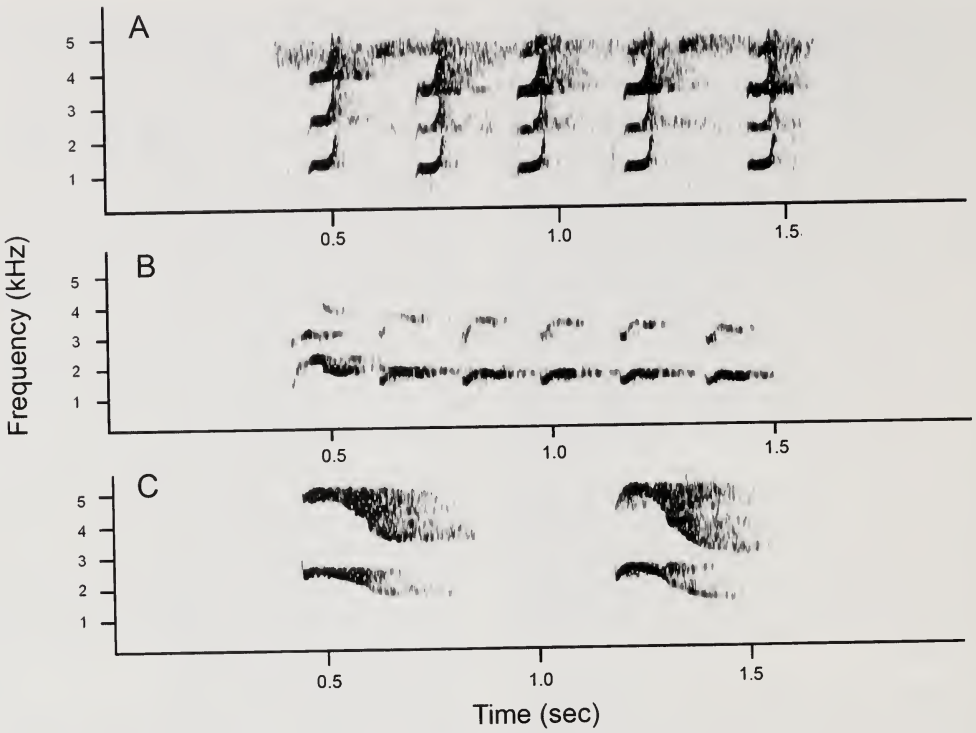


FIG. 2. Three call types of the Rufous Twistwing: (A) Vocalization #1 (ML 124448), an agitation call, (B) Vocalization #2 (ML 124453), apparently the song, and (C) Vocalization #3 (ML 124454), the *pyew* call.

ture. Vocalization #1 at times is given by agitated birds as a single note (ML 128954).

Vocalization #2 was recorded once at Oceanía (ML 124452) and heard four times at Extrema (ML 124453). It consists of a loud chiming series of 5–7 evenly paced notes, descending in pitch, with the first note more disyllabic, ringing and prolonged than subsequent notes (n = 11 calls, from 3 bouts of calling by 2 individuals; Table 2, Fig. 2B).

TABLE 2. Acoustic properties (mean ± SD) for known vocalizations of the Rufous Twistwing.

Parameter	Vocalizations[d]		
	# 1[a]	# 2[b]	# 3[c]
Overall duration, sec	0.97 ± 0.57	1.12 ± 0.13	0.33 ± 0.05
Duration of first note, sec	0.07 ± 0.01	0.15 ± 0.02	
Duration of mid-note, sec	0.07 ± 0.01	0.09 ± 0.01	
Duration of final note, sec	0.07 ± 0.01	0.11 ± 0.01	
Number of notes	6.5 ± 4.3	6.4 ± 0.8	1.0
Note rate, notes/sec	6.5 ± 1.01	5.9 ± 0.11	
Call rate, calls/min	13.8 ± 8.9	5.7 ± 2.3	7.1 ± 7.8
Max frequency, kHz	5.0 ± 0.3	2.20 ± 0.19	5.19 ± 0.13
Min frequency, kHz	1.01 ± 0.10	1.14 ± 0.06	1.55 ± 0.10
Bandwidth, kHz	4.0 ± 0.29	1.01 ± 0.25	3.64 ± 0.16
Number of calls measured	30	11	13

[a] Data from ML 124448 (locality: Oceanía, Peru; recordist: MJA), ML 124449 (locality: Oceanía, Peru; recordist: MJA), and ML 124455 (locality: Extrema, Bolivia; recordist: JAT).
[b] Data from ML 124452 (locality: Oceanía, Peru; recordist: PAH) and ML 124453 (locality: Extrema, Bolivia; recordist: JAT).
[c] Data from ML 124454 (locality: Extrema, Bolivia; recordist: NS).
[d] Harmonics were included in measurements for Vocalizations # 1 and # 3, but ignored for Vocalization # 2 where they were much weaker.

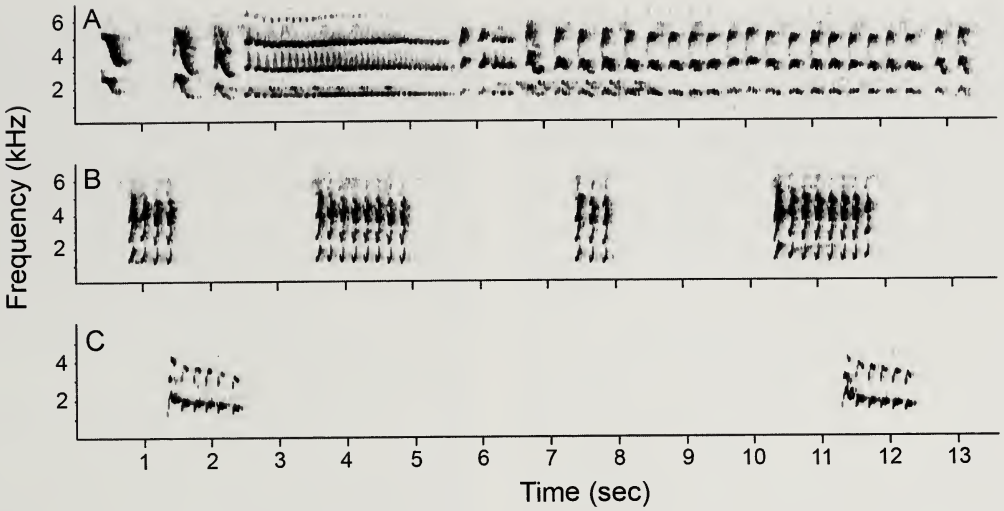


FIG. 3. Sonograms, showing delivery pattern over longer time-frames, of (A) Vocalization #3, followed by a 'long call', (B) a subdued version of Vocalization #1 (ML 124455), and (C) Vocalization #2, all given by a single individual at Extrema, Dpto. Pando, Bolivia.

The individual notes have only two, rarely three, harmonics. The typical phrase is more stereotypic than Vocalization #1 and, at a rate of 5.7 ± 2.3 calls/min, is distinctly slower (Fig. 3B, C). It is at times reminiscent in emphasis and pattern to the song of the Buff-throated Foliage-gleaner (*Automolus ochrolaemus*).

Vocalization #3 was a loud whistle (*pyew*). It was heard during two encounters at Oceanía and Extrema. Analysis of a sample (n = 13 calls, from three bouts by one individual at Extrema) indicates this call consists of a fundamental note with a single strong harmonic, given alone or in couplets (Table 2, Fig. 2C). Occasionally, Vocalization #3 was given in a triplet followed by a series of trills lasting over 10 sec (ML 124454, Fig. 3A). These trills are, at times, given without an introduction by Vocalization #3 (e.g., ML 128955) and seem to be an accelerated version of Vocalization #1.

The functional significance of these vocalizations is not known. Vocalization #1 appears to be an agitation call, Vocalization #2 is probably the song, and Vocalization #3 can be described as a 'short call'. Vocalizations #2 and #3 have not previously been described and appear most likely to function in courtship. The most stereotyped call type is Vocalization #2 (Fig. 2B), which was given at regular intervals (Fig. 3C); it differs in structure and regularity from non-stereotyped agitation calls (Vocalization #1: Figs. 2A, 3B).

The Rufous Twistwing vocalized frequently at Oceanía and Extrema with Vocalization #1 heard throughout the day, especially between dawn (~0530 hrs) and ~0800 hrs. Calls were generally given in short bursts interspersed with long periods of silence but, at times, individuals called more or less consistently for periods up to 1 hr. At least two birds were heard counter-calling on one occasion at Oceanía between ~1610 and 1700 hrs. One individual at Extrema called intermittently in response to playback for several hours in the same area. All calls were given from low perches, 1–3 m above ground.

Playback of Vocalization #1 at times (2/7 trials) resulted in noisy and aggressive behavior, including flights around the source of the playback, and loud vocalizing. More often, however, playback of Vocalization #1 elicited no response or slight response (5/7 trials). Three playbacks of Vocalization #2 elicited a stronger response than Vocalization #1; all recipients approached slowly and vocalized loudly with the same call type. On one occasion, playback of Vocalization #2 resulted in repeated production of Vocalization #3.

Sociality and Mating System.—We observed two individual Rufous Twistwings to-

gether on three occasions, twice at Oceanía and once at Extrema. At least two birds were calling simultaneously within ~25 m of each other in the afternoon of 11 October 2004 at Oceanía and, the following day, two individuals were captured nearby in mist nets. The alarm calls of one bird drew the second into the net suggesting some cohesion between the two birds, both of which appeared to be males (with modified primaries).

Playbacks at Extrema resulted in two individuals giving Vocalization #1 within 15 m of the observer and within 10 m of each other. The birds were not seen side-by-side and one individual (a male) contributed virtually all vocalizations. It was unclear whether these observations related to pairs, neighbors, or cooperative males near a calling post. It is possible two males were involved, or that repeated playback and response to playback attracted a female.

One (or two) Rufous Twistwings at Extrema were vocal in a small (30 m^2) area of tall bamboo over a period of 4 days; at least one individual spent much of each day in the vicinity. Three or four vocal individuals at Oceanía appeared to call regularly from the central dense portion of the site with calling birds appearing to be relatively clumped in distribution.

DISCUSSION

Our results increase the known range of the Rufous Twistwing and confirm its presence in Bolivia and Brazil. The five sites from which the species was known prior to our study were distributed in two clusters in Peru (Lane et al. 2007) producing a total range of 3,400 km^2. Adding the new localities presented here increases the known global range to ~89,000 km^2 (Fig. 1). Our findings are consistent with the hypothesis that the species is a *Guadua* bamboo specialist distributed throughout southwest Amazonian bamboo forests, as predicted by Lane et al. (2007). Dense young secondary forest is also used by the species, usually in the vicinity of bamboo.

A sighting from Tambopata, Peru (Michael Kessler, pers. comm.) in 1984, 6 years before the type specimen was collected at Pakitza, becomes the first report of the species. The first record for Brazil is also reported retrospectively. EG took a series of in-hand photographs of a puzzling bird mist netted at Rio Branco in 1998 and distributed them at the Brazilian Ornithology Congress (Rio de Janeiro) in the same year. Participants of the congress reached a consensus that it was a Brownish Twistwing and it was so listed in a paper about the avifauna of Parque Zoobotânico (Guilherme 2001). AA and EG re-examined the evidence in February 2006 including another specimen collected at the same site in 2003. They exchanged digital images with D. F. Lane, who confirmed that both records involved the Rufous Twistwing.

The two species of *Cnipodectes* presumably overlap in distribution with the Brownish Twistwing occurring north and south of the range of the Rufous Twistwing. To the north, the Brownish Twistwing occurs from Central America to lowland Amazonia south of the Amazon River (Meyer de Schauensee 1966, Lane et al. 2007); it is also known from the humid forests of Dpto. Pando, Bolivia (Montambault 2002, Moskovits et al. 2003) including Camino Mucden (Parker and Remsen 1987), ~50 km from Extrema. This widespread form inhabits the tangled lower growth of *terra firme* forest throughout much of its range, the only exception being in Bolivia where it was repeatedly encountered in *Guadua* bamboo at Camino Mucden (Parker and Remsen 1987). Bamboo, some of it extensive, was surveyed in October 1999 at San Sebastián (11° 24′ S, 69° 01′ W) on the Río Tahuamanu and Palmera (11° 30′ S, 69° 03′ W) on the Río Muyumanu, Dpto. Pando, Bolivia (Alverson et al. 2000). Both sites are ~30 km southeast of Extrema, but no species of *Cnipodectes* was found. The apparent convergence in habitat requirements of Brownish Twistwing and Rufous Twistwing near the point of contact deserves further study.

The Rufous Twistwing is generally scarce and has been difficult to relocate at some sites (Lane et al. 2007). It has been reported only once at the intensively studied locality of Tambopata, and once during >250 hrs of field work at Estação Ecológica do Rio Acre. In addition, it is the only regional bamboo specialist that has not been recorded during 7 years of intensive fieldwork at CICRA. This absence is particularly of interest as the site contains extensive bamboo patches supporting all 19 of Kratter's (1997) bamboo specialist

birds (obligate, near-obligate, and facultative), along with six other bird species strongly or seasonally associated with bamboo in this region. These results suggest the species is relatively specialized, or confined to larger or older blocks of habitat, as suggested by Lane et al. (2007).

Results from three sites indicate the Rufous Twistwing can be relatively common and easily encountered, especially when vocalizing. We recorded it 19 times in an 8-day survey at Oceanía and 11 times in a 4-day survey at Extrema suggesting that, at least in optimum habitat, encounter rates can be fairly high. Consistent captures at Rio Branco also indicate that some populations can be sedentary for periods of several years in suitable habitat. Overall, our data suggest that populations are patchy and unpredictable, and vary widely in density.

The Rufous Twistwing is known to sally from perches to catch insects and to lift one or other of its wings repeatedly (Lane et al. 2007). Our results affirm that wing raising is a common behavior in this species and suggest that wing raises tend to be given in one-sided bouts. The function of wing raises in this species and several other genera of tyrant-flycatcher remains unclear. They may serve as signals in intersexual contexts, although they are often given by solitary birds.

The function of modified primaries in both *Cnipodectes* species has not been fully explained, but primaries presumably are used in sound production (Zimmer 1939, Ridgely and Greenfield 2001, Lane et al. 2007). The wings of the male Brownish Twistwing make an audible mechanical *pr'r'r'r'r'* wing-rattle in flight (Hilty and Brown 1986) and a similar sound has been heard from the Rufous Twistwing (Lane et al. 2007). It is likely that sound production in both species is prominent during courtship display, as in other understory birds with modified wing feathers, i.e., *Pipra* manakins and *Smithornis* broadbills, for example.

The Rufous Twistwing is more often heard than seen. The only vocalization previously reported is an agitation call which closely resembles an aggressive call of the Brownish Twistwing recorded in Ecuador (Krabbe and Nilsson 2003). Our vocal data enlarge the known repertoire of the Rufous Twistwing to at least three call types. In addition to the agitation call (Vocalization #1) noted by Lane et al. (2007), we describe a 5–7 note song (Vocalization #2), and a 1–3 note *pyew* call (Vocalization #3). One Rufous Twistwing at Extrema, Bolivia responded strongly to playback of Vocalization #2 and gave this call-type from a small area over 3 consecutive days, suggesting that it functions in advertising and courtship.

The song of the Brownish Twistwing contains 1–3 notes (Fig. 3C in Lane et al. 2007). It is perhaps analogous to the Rufous Twistwing's *pyew* call (Vocalization #3), which is also given 1–3 times in succession (Fig. 2C, double version and Fig. 3A, triple version). A relationship between the *pyew* note of the Rufous Twistwing (Fig. 2C) and the song of the Brownish Twistwing (Fig. 2D in Lane et al. 2007) is suggested by similarities in their structure; both have a 2 kHz fundamental with one major harmonic and a ridge-shaped introduction which leads into a level section. However, we believe it is unlikely the *pyew* note is the main song of the Rufous Twistwing as it is given rarely and from random points.

Vocalization #2 is given at shorter intervals from fixed points and may be analogous to the stereotyped song of the Brownish Twistwing, although it is a longer, faster series of notes. The Rufous Twistwing does not appear to give an upwardly inflected *cueet* or *kuuuu-wit* note, the unsolicited single-note call of the Brownish Twistwing (Fig. 3D in Lane et al. 2007). It is possible the *pyew* call (Vocalization #3) is homologous with the *cueet* call. This conclusion is supported by our observation that both calls are given at fairly long and irregular intervals.

The vocal repertoire of the Rufous Twistwing is similar to the Brownish Twistwing. However, presumed homologous vocalizations are diagnosably different between the two forms supporting their treatment as separate species. They may produce different mechanical noise; songs of the Brownish Twistwing are often introduced by bill snapping sounds (Hilty and Brown 1986), which have not yet been reported for the Rufous Twistwing. The wing-rattles of the two species have not been compared.

Male Brownish Twistwings sing from habitual song posts and do not appear to defend

pair-territories (Parker and Remsen 1987). They therefore differ from males of most tyrant-flycatchers and resemble those of certain manakin genera (e.g., *Neopelma* and *Tyranneutes*) with polygamous breeding systems. Our observations suggest the behavior of male Rufous Twistwing is similar. The sexual size dimorphism in both *Cnipodectes* species is extreme for tyrant-flycatchers (Lane et al. 2007), again suggesting polygamy. Further research is required to clarify breeding biology and ranging behavior in *Cnipodectes*.

CONSERVATION STATUS

We estimate a global range of ~89,000 km^2 on the basis of all 13 known localities for the Rufous Twistwing (Fig. 1). However, our results fit the prediction of Lane et al. (2007) that the global range coincides with the discontinuous block of *Guadua*–dominated forest that extends over much of southeastern Peru, northern Bolivia, and western Amazonian Brazil. The total area of this habitat is unknown, but has been estimated at ~121,000 km^2 (Nelson 1994) to ~180,000 km^2 (Saatchi et al. 2000).

The Rufous Twistwing is probably the least abundant and perhaps the most threatened of all bamboo specialists in Amazonia. The risk of extinction in the short term is low but recent development projects, including the paved Trans-Oceanica Highway, will increase human settlement and habitat destruction in the region (Nepstad et al. 2001, Conover 2003, Tobias and Brightsmith 2007). This may not be detrimental to the Rufous Twistwing because *Guadua* bamboo at times proliferates on deforested land and abandoned *chacras* (Griscom and Ashton 2003; D. F. Lane, pers. comm.), thereby increasing suitable habitat for the species. We note, however, that it is usually recorded in large, mature patches of *Guadua* bamboo and appears to be absent from stretches of more recent *Guadua* regrowth along the proposed route of the Trans-Oceanica Highway. We also note the socioeconomic value of large bamboos and the increasing tendency to harvest them (Bystriakova et al. 2004). These factors suggest the extent of suitable habitat for the species may decline in the future.

The Rufous Twistwing is more or less restricted to patchy bamboo forests. It is generally scarce, and we have shown it to be absent from some apparently suitable sites. More field data are needed before population size can be calculated but, for the purpose of classifying its conservation status according to current data and IUCN guidelines (IUCN 2001), we estimate this species may have a declining global population of <10,000 individuals, and that all subpopulations may contain fewer than 1,000 individuals. We therefore recommend that it be listed on the IUCN Red List as Vulnerable under criterion C2a (i) (IUCN 2001) with a caveat that data quality is poor and that further surveys may lead to future changes in status. Only a small part of the proposed distribution of the Rufous Twistwing has been surveyed and the threat from habitat disturbance remains unclear. Field surveys are required throughout the bamboo forests of southwest Amazonia and the extent of bamboo should be assessed at intervals, perhaps through remote sensing techniques.

ACKNOWLEDGMENTS

Permission for field work was granted in Peru by Instituto Nacional de Recursos Naturales (INRENA) and in Brazil by Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). Logistical support and/or funding was provided by SOS Amazônia and WWF-Brazil (to Alexandre Aleixo), and Centro Nacional de Pesquisa para Conservação das Aves Silvestres (CEMAVE) (to Edson Guilherme). We are indebted to Macaulay Library for loan of sound recording equipment, and to N. C. A. Pitman and R. B. Huayllapuma for logistical support. We thank J. M. Barnett, S. H. M. Butchart, C. D. Cadena, N. G. Gerhart (deceased), Michael Kessler, D. F. Lane, P. C. Pulgarín R., Marcos Pérsio D. Santos, G. P. Servat, and Thomas Valqui for useful data, comments, and corrections. Fieldwork was funded in part by a Fulbright grant (to D. J. Lebbin), a CNPq/SECTAM joint Regional Development Research Program research grant #35.0415/2004-8 (to Alexandre Aleixo), and a Junior Research Fellowship from Newnham College, University of Cambridge (to Nathalie Seddon).

LITERATURE CITED

Alverson, W. S., D. K. Moskovits, and J. M. Shopland (Editors). 2000. Bolivia: Pando, Río Tahuamanu. Rapid Biological Inventories Report 1. The Field Museum, Chicago, Illinois, USA.

Bystriakova, N., V. Kapos, and I. Lysenko. 2004. Bamboo biodiversity. UNEP-WCMC/INBAR, Cambridge, United Kingdom.

Conover, T. 2003. Peru's long haul: highway to riches or ruin. National Geographic June: 80–111.

Fitzpatrick, J. W. 2004. Family Tyrannidae (tyrant flycatchers). Pages 170–462 *in* Handbook of the birds of the world (J. del Hoyo, A. Elliott, and D. A. Christie, Editors). Volume 9. Cotingas to pipits and wagtails. Lynx Edicions, Barcelona, Spain.

Griscom, B. W. and P. M. S. Ashton. 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in southeastern Peru. Forest Ecology and Management 175:445–454.

Guilherme, E. 2001. Comunidade de aves do campus e Parque Zoobotânico da Universidade Federal do Acre, Brasil. Tangara 1:57–73.

Hilty, S. L. and W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, USA.

IUCN. 2001. IUCN Red List categories and criteria. Version 3.1. IUCN Species Survival Commission, Gland, Switzerland and Cambridge, United Kingdom.

Krabbe, N. and J. Nilsson. 2003. Birds of Ecuador, DVD-ROM. Bird Songs International, Westernieland, The Netherlands.

Kratter, A. W. 1997. Bamboo specialization by Amazonian birds. Biotropica 29:100–110.

Lane, D. F., G. P. Servat, T. Valqui H., and F. R. Lambert. 2007. A distinctive new species of tyrant flycatcher (Passeriformes: Tyrannidae: *Cnipodectes*) from southeastern Peru. Auk 124:762–772.

Meyer de Schauensee, R. 1966. The species of birds of South America with their distribution. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Montambault, J. R. 2002. Informes de las evaluaciones biológicas de Pampas del Heath, Alto Madidi, Bolivia, y Pando, Bolivia. Conservation International, Washington, D.C., USA.

Moskovits, D. K., W. S. Alverson, and I. Halm (Editors). 2003. Bolivia: Pando, Federico Roman, Rapid Biological Inventories 06. The Field Museum, Chicago, Illinois, USA.

Nelson, B. W. 1994. Natural forest disturbance and change in the Brazilian Amazon. Remote Sensing Reviews 10:105–125.

Nepstad, D., G. Carvalho, A. Barros, A. Alencar, J. Capobianca, J. Bishop, P. Moutinho, P. Lefebvre, S. U. Lopes, and E. Prins. 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. Forest Ecology and Management 154:395–407.

Parker, T. A. and J. V. Remsen. 1987. Fifty-two Amazonian bird species new to Bolivia. Bulletin of the British Ornithologists' Club 107:94–107.

Ridgely, R. S. R. and P. J. Greenfield. 2001. The birds of Ecuador: a field guide. Volume 2. Princeton University Press, Princeton, New Jersey, USA.

Ridgely, R. S. R. and G. Tudor. 1994. The birds of South America: the suboscine passerines. Volume 2. University of Texas Press, Austin, USA.

Saatchi, S. S., B. Nelson, E. Podest, and J. Holt. 2000. Mapping land cover types in the Amazon Basin using 1 km JERS-1 mosaic. International Journal of Remote Sensing 21:1201–1234.

Schulenberg, T. S., C. A. Marantz, and P. H. English. 2000. Voices of Amazonian birds: birds of the rainforest of southeastern Peru and northern Bolivia. Cornell Laboratory of Ornithology, Ithaca, New York, USA.

Silman, M. R., E. J. Ancaya, and J. Brinson. 2003. Los bosques de bambú en la Amazonía occidental. Pages 63–73 *in* Alto Purús: biodiversidad, conservación y manejo (R. Leite Pitman, N. Pitman, and P. Álvarez, Editors). Center for Tropical Conservation, Lima, Peru.

Tobias, J. A. and D. J. Brightsmith. 2007. Distribution, ecology and conservation status of the Blue-headed Macaw *Primolius couloni*. Biological Conservation 139:126–138.

Zimmer, J. T. 1939. Studies of Peruvian birds: notes on the genera *Myiotriccus*, *Pyrrhomyias*, *Myiophobus*, *Onychorhynchus*, *Platyrinchus*, *Cnipodectes*, *Sayornis*, and *Nuttallornis*. American Museum Novitates 1043:1–15.

The Wilson Journal of Ornithology 120(1):50–61, 2008

NATURAL HISTORY AND BEHAVIOR OF THE ALDABRA RAIL (*DRYOLIMNAS [CUVIERI] ALDABRANUS*)

ROSS M. WANLESS[1,2] AND PHILIP A. R. HOCKEY[1]

ABSTRACT.—The Aldabra Rail (*Dryolimnas [cuvieri] aldabranus*) is endemic to Aldabra Atoll, Seychelles and is the last remaining flightless bird in the tropical western Indian Ocean. We studied it over two breeding seasons from 1999 to 2001. Pairs formed strong bonds, defended territories year-round, and were mate and territory faithful across seasons. Reproductive duties are shared by males and females. Breeding was closely tied to the rainy season and pairs responded to favorable conditions by increasing clutch size and clutch frequency. Clutches contained 1–4 eggs and replacement clutches were laid if nests failed early in the season. The incubation period was 19–24 days and hatching was usually synchronous. Mayfield estimates of daily survival of eggs and nesting success were 98.8% and 77.0%, respectively. Hatching success was 60.9% and 57% of chicks that hatched were successfully reared to independence. Chicks are sub-precocial and fledged chicks were cared for in the natal territory for at least 2 months, after which they were forcibly evicted. A large repertoire of behaviors and ritualized displays are described including pseudo-copulation and reverse mounting. *Received 25 August 2006. Accepted 30 March 2007.*

The Aldabra Rail (*Dryolimnas [cuvieri] aldabranus*) is endemic to Aldabra Atoll, Seychelles. Historically, distinct representatives of the genus *Dryolimnas* occurred throughout the Aldabra Group (Aldabra and Cosmoledo atolls and Astove and Assumption islands), as well as on Madagascar and the Mascarenes (Rand 1936, Rountree et al. 1952, Benson 1967, Mourer-Chauviré et al. 1999). Only the White-throated Rail (*D. c. cuvieri*) of Madagascar and the Aldabra Rail remain—all other forms are extinct. The Aldabra Rail is truly flightless (Wanless 2003a) unlike its sister taxon on Madagascar (Rand 1936, Taylor and van Perlo 1998). The range of the Aldabra Rail had contracted by the 1970s to two islands within Aldabra (Malabar and Polymnie) and the small lagoon islet of Île aux Cèdres (Benson and Penny 1971, Collar 1993, Taylor and von Perlo 1998).

A reintroduction of Aldabra Rails to Picard Island was successfully undertaken in 1999 (Wanless et al. 2002). This provided the opportunity to study the natural history and breeding biology of the Aldabra Rail. The species received some research attention in the 1970s, but the autecological study went unpublished (Huxley 1982). We located the manuscript and received permission (C. R. Huxley, pers. comm.) to use the results to corroborate many of our findings, particularly those relating to pair behaviors. The objectives of our paper are to describe aspects of the natural history of the Aldabra Rail, including adult, juvenile, and chick plumages. We also describe use of a reliable genetic technique for ascertaining gender of Aldabra Rails, and a suite of territorial and reproductive behaviors and displays.

METHODS

Study Area.—Aldabra Atoll (9° 24′ S, 46° 20′ E) is 1,100 km southwest of the granitic Seychelles and 400 km north of Madagascar. It is a large, slightly raised coral atoll (34 × 14.5 km, land area = 155 km^2). Four large islands (Grande Terre, Malabar, Picard, and Polymnie) form a rim around a substantial, shallow lagoon that contains numerous islets (Fig. 1). The climate is dry and tropical with an average annual temperature of 27° C. Annual rainfall is variable, but averages about 1,200 mm with a pronounced wet season, usually November–April (Stoddart 1971). The vegetation is low and either dense or open mixed scrub. The former includes large, almost monospecific stands of *Pemphis acidula*. Aldabra Rails were studied mainly on Malabar and Picard islands between 1999 and 2001.

Identification of Gender.—The method for gender identification in the field using bill color (Penny and Diamond 1971) proved unre-

[1] DST-NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town, Rondebosch, South Africa 7701.

[2] Corresponding author;
e-mail: rwanless@botzoo.uct.ac.za

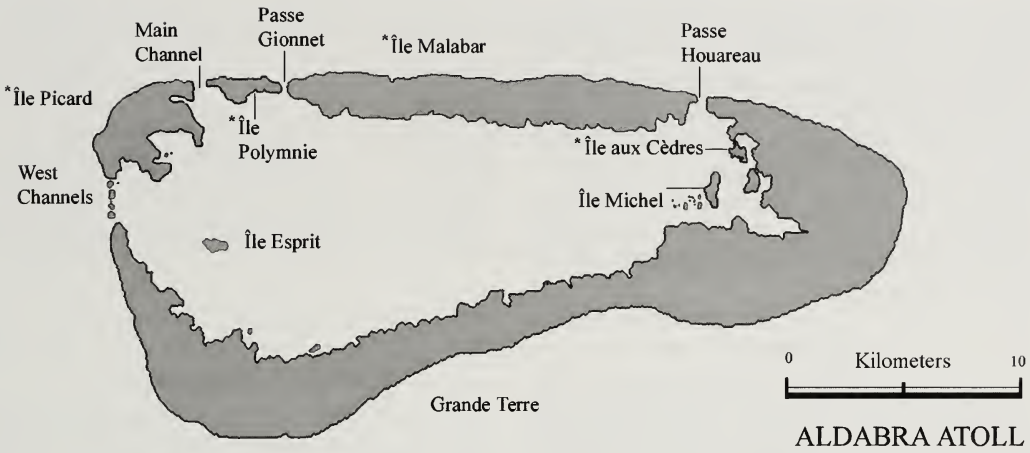


FIG. 1. Aldabra Atoll, Seychelles, showing the four rimming islands, larger lagoon islets, and the four channels to the open sea. Islands with Aldabra Rail populations are marked with asterisks.

liable based on necropsy of birds. We used a universal genetic technique (Fridolfsson and Ellegren 1999) to assign gender to all individuals that were trapped and banded. PCR blanks and positive controls were included to ensure reliable reactions. We compared bill and tarsus length measurements from 22 males and 22 females to investigate sexual dimorphism. Differences were tested with a *t*-test at the 0.05 significance level. Gender of birds was also assigned when handled following Penny and Diamond (1971), and the results were compared to with genetic identification.

Breeding Biology.—The location and construction materials of 23 active Aldabra Rail nests and the dimensions of nine were recorded. Elevation was measured from the ground to the base of the nest. Nest length (longest axis) and width were measured to the nearest 5 mm across the centre of the cup. Cup depth was measured vertically from the deepest part of the nest to the cup rim.

Eggs were measured to the nearest 0.1 mm using vernier callipers and weighed to the nearest 0.5 g using a 100 g Pesola spring balance. Many eggs were of unknown age and weights should be treated with caution.

Average clutch size was estimated from nests visited at least twice during incubation. In instances when nests were not found, but newly hatched chicks were located, a minimum estimate of clutch size was assumed to equal the number of chicks. The response of birds to favorable conditions was examined by comparing clutch size and number of repeat clutches between the reintroduced population on Picard (no density-dependent constraints on reproduction) and on Malabar (high density-dependence) (Wanless et al. 2002). Where appropriate, means ± one standard deviation are presented.

We performed a Kaplan-Meier survival function analysis (which calculates the cumulative proportion of nests surviving over time) for the incubation period with survival censored at 20 days (Nur et al. 2004). Hatching success was calculated from complete clutches only. We estimated the daily survival rate for eggs and nest success for the incubation period following Mayfield (1975): daily survival = $1 - losses/e$ and nest success = $(\text{daily nest survival})^{ip}$, where e = exposure, the total number of active days per egg/nest, and ip is the incubation period. A nest was defined as successful if at least one chick fledged. We considered chicks in full juvenile plumage and capable of foraging for themselves to have been reared to independence. Chick survival is the number of chicks reared to independence divided by the number that hatched and breeding success is the number of chicks reared to independence per nesting attempt.

Behavior.—We took detailed notes in the field describing interactions between birds. Particular attention was given to posture and the role of the white throat patch and undertail

coverts in displays. Birds were also photographed in various postures from which line drawings were produced. Interactions were either common (e.g., pairs duetting and greeting) or only seen opportunistically (e.g., mating). Consequently, no attempts were made to quantify the relative frequency or individual variation of behaviors, but Huxley's (1982) findings were incorporated or used to corroborate our observations.

RESULTS

Structure and Plumage.—The Aldabra Rail is a medium-sized rail with somewhat reduced wings that do not extend beyond the tail at rest. The body is slender, emphasized by the noticeable reduction of breast musculature. The upper parts are a dark, olive green, and the white throat patch contrasts strongly with the dark body plumage. The undertail coverts are also white. The bill is black, long, slender, and sharply pointed with the base variably pink or red. The head, neck, and breast of adults from Malabar and Polymnie are rich, dark, and red-brown with the flanks barred with white. Adults from Île aux Cèdres are noticeably duller, paler, and tinged with pink.

Newly hatched chicks are typical of rallids, being thickly covered with black down. Primary feathers begin to emerge from their sheaths at about 2 weeks. Juveniles resemble adults but are duller with reduced contrast between upper and lower body coloration.

Identification of Gender.—The gender of 47 (81%) of 58 adults ascertained in the field was confirmed to be correct by genetic analysis; of the remaining 11 birds, six males were incorrectly identified as females and five females as males. Males were significantly larger than females in bill length (43.5 ± 2.7 vs. 39.4 ± 1.5 mm, df = 42, $P < 0.001$) and tarsus length (45.4 ± 5.7 vs. 41.3 ± 1.3 mm, df = 42, $P = 0.007$). However, there was overlap between large females and small males in both measures (Fig. 2), and we conclude that gender of Aldabra Rails cannot be reliably identified in the field or in the hand.

General Ecology.—Paired birds roosted on the ground, usually less than 10 m apart, and were diurnal becoming active at first light by immediately performing a duet. This was frequently echoed by other nearby pairs in a domino effect. Occasionally, birds called or pairs duetted in the middle of the night.

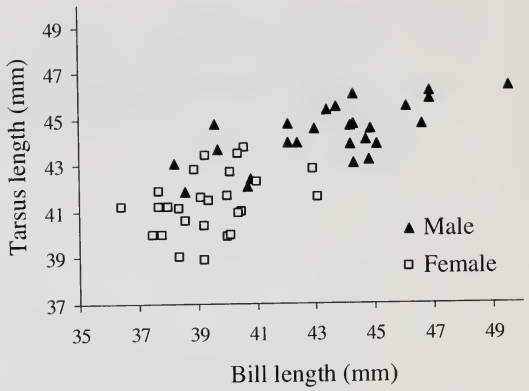


FIG. 2. Sexual dimorphism in correlated morphological characters of the Aldabra Rail from 22 adult females and 22 adult males.

Aldabra Rails use their bills to remove leaf litter, probe soil, and catch food; the feet were not used to scratch in litter or to manipulate food. Size of prey items was, in most cases, too small to estimate and no identifiable remains were found in fecal samples. A single regurgitation contained finely crushed arthropod exoskeleton(s) and 18 tiny land-snail shells. The latter might have been ingested as grit to aid digestion. Aldabra Rails hunted geckos, skinks, and crabs opportunistically. These prey were held in the bill when captured, while the bird alternately flicked its head rapidly from side to side and then beat the prey against the ground or a branch. Larger crabs were killed by rapid, powerful blows with the bill directed between the eyes. Crab exoskeletons and hermit crab shells were broken open by placing them on the ground and repeatedly hammering them from above. Rails washed large food items if water was nearby.

Breeding Biology.—Courtship behavior prior to pair formation has not been reported. New pair formation occurred within 5 days after reintroduction to Picard Island, but could have happened earlier. Aldabra Rails are monogamous and both males and females defended the territory year-round. Territory fidelity between years was high; of 14 pairs on Picard Island where both individuals were color-banded, only two pairs were suspected of having shifted territory. Males and females shared incubation and chick-provisioning du-

TABLE 1. Clutch sizes and breeding success (defined as chicks reared to independence per nest) of Aldabra Rails. ND denotes no data.

Parameter	Total nests (eggs)	Mean clutch size	Total hatched	Chick survival	Breeding success
All clutches (Picard and Malabar)	23 (65)	2.83	ND	ND	1.11
All clutches (Picard only)	17 (51)	3.0	30	20	1.05
First clutches (Picard only)	9 (28)	3.11	21	14	1.27
Repeat clutches (Picard only)	8 (23)	2.88	9	6	0.75

ties. There was no evidence of cooperative breeding in the species and young were invariably evicted from the natal territory, usually at 8–10 weeks of age, once they had attained full juvenile plumage.

The most conspicuous pair behavior was the duet, which consists of a series of loud, high-pitched, ascending whistles that increase in pitch to a sustained crescendo. Duets were given after a territorial dispute, after the *Greeting Display*, or in response to other pairs duetting nearby. We interpret duetting as an integral part of pair-bonding behavior. Pair-bonding activities were increasingly noticeable as the breeding season approached. Duetting and response to playback of duets were noticeably reduced during chick rearing, and other pair-bonding behaviors were seldom seen.

Nesting Ecology.—Nest site prospecting began in November or early December and males did most of the building. Two or more nests may be built and material was often placed in several potential sites. Once a site was selected, one or both birds stood on or near the site and gave a series of low, groaning *crreaak* calls.

Eight of 23 active nests were on the ground; the other 15 were in low shrubs, *Pandanus tectorius* bushes, or natural cavities in trees. Elevated nests ranged from barely above ground to 1.6 m above ground (mean = 0.8 m, n = 14). Only 1 of 23 nests lacked some overhead shelter.

A wide diversity of dry plant material (usually the dominant litter of the area) was used in nest construction. Two active nests, however, had almost no added material and were natural depressions (under a shrub and in a tree cavity, respectively), sparsely lined with dry grasses or *Casuarina* needles.

Nests were usually constrained by the nature of the site, but most were quite large and roughly circular (260 ± 33 × 221 ± 22 mm, n = 23). The mean depth was 116 ± 61 mm (n = 9). The mean cup length was 149 ± 22 mm, mean width was 134 ± 27 mm and the mean depth was 48 ± 24 mm (n = 9 for all cup measurements). The cup was usually sufficiently deep that only the head of an incubating adult protruded; the adult's black-streaked, dull olive-green back camouflaged it well on the nest. Three pairs used brooding nests to brood downy chicks; others may have gone undetected. These were built on the ground under shelter and consisted of a shallow cup lined with a thin layer of dry material.

Mean egg dimensions were 43.3 ± 1.2 × 30.6 ± 1.1 mm, and mean mass was 21.4 ± 2.1 g (n = 39). Eggs varied in shape, but most were elliptical or biconical. The moderately glossy, off-white shell is covered in maroon-brown speckling and has a finely granulated surface. Speckling is most dense at the obtuse end and many speckles are clouded or adumbrated, giving a multi-toned appearance.

Twenty-three clutches were monitored from egg-laying or incubation to completion (Table 1). Small unequal sample sizes and the non-independence of samples (repeat clutches) prevented testing for differences in mean clutch size between the reintroduced population from Picard and the source population on Malabar. Average clutch sizes were slightly larger on Picard (3.0, range 2–4 eggs, n = 17) than on Malabar (2.33, range 1–3 eggs, n = 6). Excluding repeat clutches increased mean clutch size on Picard to 3.11 eggs (n = 9 nests).

Six pairs on Picard attempted second clutches after successfully rearing chicks, four of which were successful. Two pairs laid third clutches, both of which failed at the egg stage (Guy Esparon, pers. comm.). A pair on Malabar in 2000/2001 built a new nest and laid immediately after their first clutch was dep-

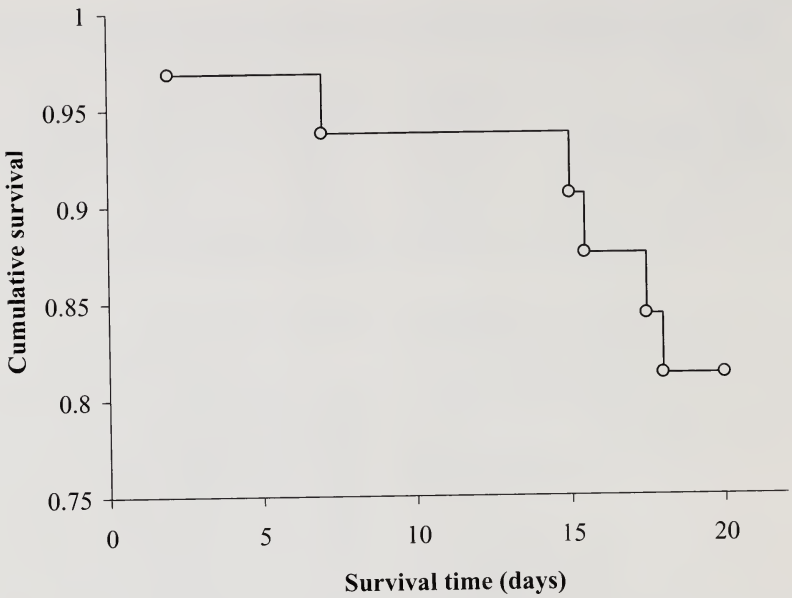


FIG. 3. Kaplan-Meier survival probabilities for Aldabra Rail eggs in the 2000/2001 breeding season with all data censored at 20 days.

redated; we found no other repeat clutches on Malabar.

Timing of rail reproduction was closely tied to onset of the wet monsoon and concomitant increase in invertebrate densities. Laying of first clutches in the 2000/2001 breeding season on Picard was concentrated around the end of December and early January, although one successful clutch was laid in mid-November, before the monsoon began. Eggs were laid at intervals of 1–4 days, typically every other day.

The incubation period (from last egg to first-hatched chick) was 19–24 days (mean = 21.2 days, n = 5 nests). Individual eggs took 22–24 days from laying to hatching (mean = 22.6 days, mode = 22 days, n = 11 eggs). The hatching interval was 0–3 days, synchrony being the norm, implying that incubation typically starts after clutch completion. Chicks are semi-precocial (*sensu* Starck and Ricklefs 1998); they hatch downy and are able to follow parents from hatching onwards. They can leave the nest within a few hours of hatching and abandoned the nest within 3 days. Eggshells were not found and one female was observed to eat the hatched egg shells. Infertile eggs were abandoned in the nest (n = 2). Newly hatched chicks left the nest for periods in the care of one parent when infertile or late-developing eggs were being incubated. Repeat clutches were timed so that juveniles from the first brood were evicted from the territory before the next clutch hatched (n = 6). Parents adopted one of two caring and provisioning strategies once the nest was abandoned. They either divided the brood between themselves and provisioned young independently, or they left chicks well concealed, foraged alone, and returned to the chicks with food. The latter strategy was only used for downy chicks. Downy chicks often gave a continuous, high-pitched *peep* begging call while following foraging adults. Chicks immediately ran to the nearest dark place when parents gave a danger call. Parents provisioned chicks until they were 6–8 weeks of age and became aggressive towards chicks when they attained full juvenile plumage, at ~8 weeks of age. Aggressive interactions continued until offspring left the natal territory (generally at 8–10 weeks of age).

Two of 12 nests found during incubation failed to produce any chicks. The Kaplan-Meier survival function for eggs (Fig. 3) showed relatively low failure rate due to predation. The overall survival rate was inflated because eggs that were infertile but survived

beyond 20 days were not counted as failures in the analysis. Overall, the daily survival rate of eggs was 97.5% and the Mayfield estimate of nest success during incubation was 77.0%. Hatching success was 60.9% (28 of 46 eggs from 15 complete clutches). The 18 eggs that failed did so because of presumed predation (7), breakage (3), and presumed infertility/other causes (8). Only one nest (containing 2 eggs) was entirely depredated: all other predation events involved the loss of single eggs. Chick survival was 57% with 16 of 28 hatchlings surviving to independence. Breeding success on Picard was 1.05 chicks per nesting attempt (n = 17 attempts), although breeding success of repeat clutches following successful first clutches was only 0.75 chicks per nesting attempt (n = 8 attempts, Table 1).

Behavior.—Adult Aldabra Rails used a variety of vocalizations, postures, and displays, mostly in territorial or sexual contexts. Two prominent plumage features, the white throat patch and white undertail coverts, had particular significance in postures and displays. These features contrast strongly with the darker plumage of the rest of the bird and also stand out against the surroundings of the understory.

The *Relaxed Posture* was used when resting, foraging, and walking. When standing, the neck was bent or retracted with the head pointing horizontally or down, hiding the throat patch. The tail was flicked with each step, but the undertail coverts were not fanned. There were no associated vocalizations except during the early breeding period when males mate-guard and both males and females gave the *mpclick* call continuously and partially displayed the undertail coverts. When sleeping, the head and neck were pulled in and the bill held horizontally, at times while the bird stood on one leg.

Aldabra Rails bathed regularly if fresh water was available. Bathing was done in shallow water and the head dipped repeatedly under the water in a bobbing fashion, spilling water over the upper parts on each rise and wetting the underparts on each dip. A wet bird may sun itself with the wings fanned horizontally. There are no records of alternative bathing activities (e.g., dust bathing or bathing in the sea). When preening, the eyes were kept shut. Allopreening was initiated by gently pecking around the head area. It was initiated by males or females and was also targeted at young birds. Allopreening often preceded other pair-bonding behavior such as duetting and copulation.

The *Greeting Display* (Fig. 4A) was usually performed when pairs reunited after foraging apart; they trotted towards each other with necks partially stretched and vertical, displaying their throat patches. Both gave soft, purring calls and occasionally touched bills. Once birds met, contour feathers were slightly raised and undertail coverts fanned, but the white throat patch was concealed by the low head position and retracted neck.

The *Singing Posture* (Fig. 4B) was used by individuals when calling singly and when duetting. Birds often ran towards each other when duetting and stood close. The bill was held slightly below horizontal and the neck stretched and angled forward and upwards. The body was angled slightly upwards and the legs held in a partial crouch. Calls were variable in length; after calling, birds usually adopted the *Relaxed Posture.*

The *Curious Posture* (Fig. 4C) was given when a rail encountered a novel stimulus such as humans and/or their equipment. The context was similar to that of the *Alert Posture*, although the latter was used when a bird's attention was drawn to something further away, such as when territorial intruders were detected. The neck was stretched and held horizontal. The body was also horizontal and the head at times cocked at an angle. The neck was often retracted and extended at a new angle. The legs were at times in a half-crouch, as if ready to flee. The contour feathers were not raised.

The *Alert Posture* was adopted when a bird was in a similar state of arousal as for the *Curious Posture*, but was not restricted to investigating novel stimuli. It is similar to the *Upright Posture*, but the undertail coverts were not displayed. The body was upright with the neck fully or partially stretched and the throat patch partially obscured. The tail pointed down and coverts and contour feathers were not fanned.

The *Territorial Defense Display* (Fig. 4D) was given when a conspecific intruded on a territory or in a boundary dispute. The body was horizontal and the neck pulled in, par-

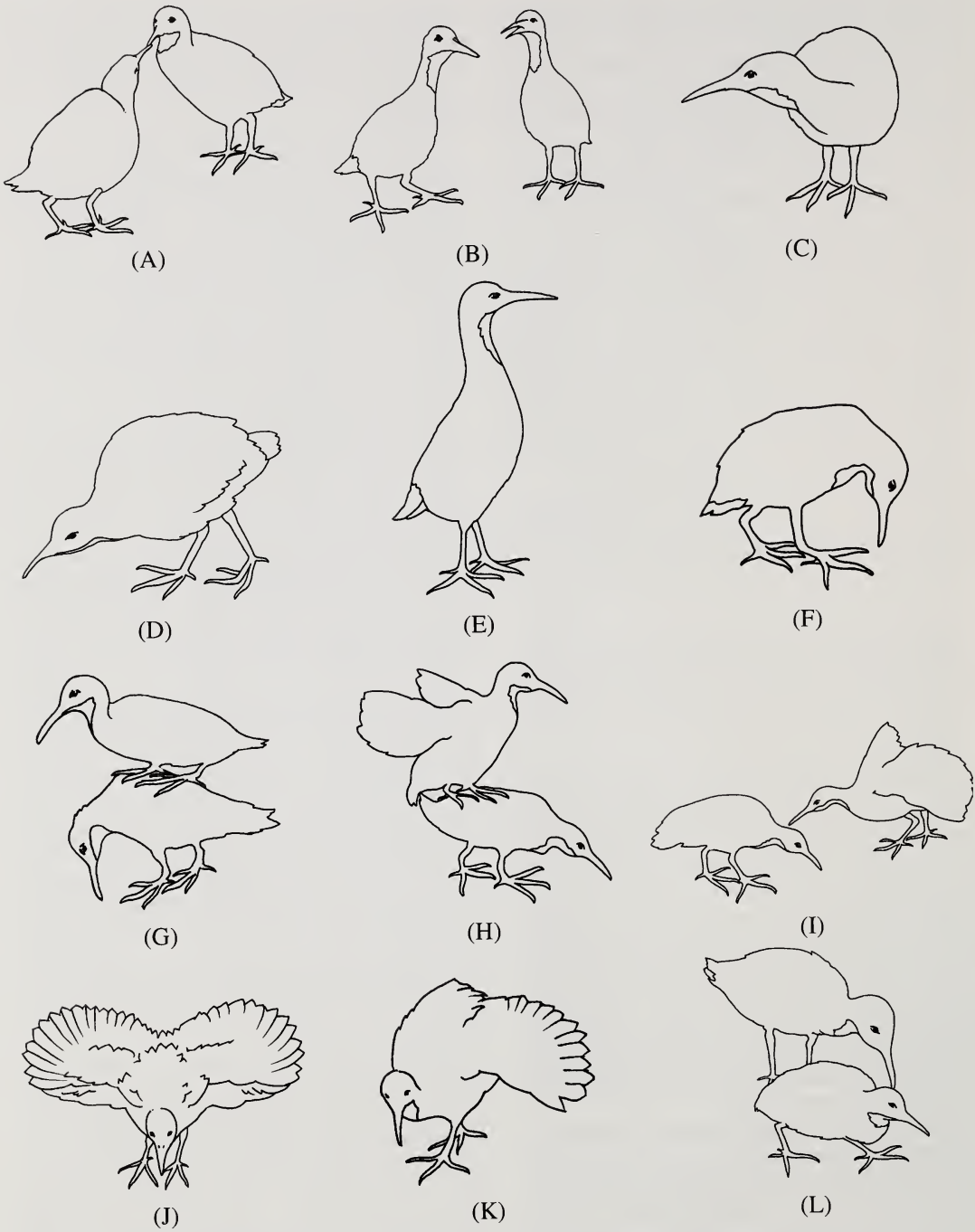


FIG. 4. Postures and displays of the Aldabra Rail based on photographs and field observations. (A) *Greeting Display*, (B) *Singing Posture*, (C) *Curious Posture*, (D) *Territorial Defense Display*, (E) *Upright Posture*, (F) *Invitation Display*, (G) *Mounting*, (H) Coitus, (I) *Post-copulatory Display*, (J) *Full Nest Defense Display*, (K) *Partial Nest Defense Display*, and (L) *Aggressive and Submissive displays.*

tially obscuring the throat patch. The tail was raised, coverts fully fanned, and the contour feathers were all raised. Wings were occasionally held slightly away from the body with primaries partially splayed. Birds approached each other and moved from side to side, flicking the tail with each step. If neither protagonist retreated, they adopted the *Upright Posture* and typically a fight ensued.

The *Upright Posture* (Fig. 4E) was also used in the context of territorial defense. The body was upright and the neck fully extended and held vertically, displaying the throat patch. The tail was held horizontal or pointing slightly downwards with coverts fully fanned. Contour feathers were slightly raised on occasions. It was used during *Aggression Displays* by the aggressor. After the *Upright Posture* was adopted by one or both individuals, if one bird backed down it was usually chased, if not, they fought. Chasing birds held their necks up and out and displayed their throat patches and undertail coverts, whereas fleeing birds kept the tail down, concealing the undertail coverts. Chasing birds flapped their wings to assist in maneuvering. The *Chasing Posture* was also used by adults when evicting their offspring from the natal territory and, in a trespassing situation, against neighbors or their offspring. The pursuing bird pecked the fleeing bird whenever it could reach it.

Birds circled each other as a prelude to fighting or approached head-on in the *Territorial Defense Stance.* They then suddenly adopted the *Upright Posture* (fully displaying their throat patch) and attacked, leaping and kicking each other simultaneously, while flapping their wings vigorously and directing blows with their bills. They either landed on their feet and repeatedly circled and jumped at each other, alternating between the *Upright* and *Territorial Defense Postures*, or they fell to the ground, facing each other while balancing on their tails and wings and kicking vigorously. Fights were violent and occasionally resulted in serious injury or death.

A series of postures was used before, during, and after copulation. The sequence of events appeared to be fixed with the exception of the initiation. Incomplete events may have been due to the presence of observers, but we believe mounting was a pair-bonding activity; when cloacal contact was absent, the behavior is referred to as *Pseudo-copulation. Pseudo-copulation* was frequent in the months before reproduction began and after young had left the natal territory.

Copulation was usually preceded by duetting. It was initiated in one of two ways. Birds adopted the *Approach Posture*, moved towards their mates with the neck stretched vertically, body angled up (but not as much as in the *Upright Posture*), displaying the throat patch and undertail coverts. Alternatively, initiation of the sequence began when a bird faced away from its mate and performed the *Invitation Display* (Fig. 4F). This was present in all copulation sequences observed. A bird in the *Invitation Display* arched its neck and pointed the bill downwards. The body was angled upwards and the bird waddles forward a few paces in a half crouch, slowing quickly to a standstill. The tail was pointed down, the undertail coverts fanned and the wings folded. A responsive mate adopted the *Approach Posture,* walked or trotted towards its mate, and then mounted the inviting bird (Fig. 4G). It then crouched on the latter's back, the body almost horizontal, tarsi touching the other bird's back, the head pointing down at 45°, with wings folded and the undertail coverts fully fanned. The mounted bird then raised its tail while displaying the undertail coverts. The head and neck positions changed repeatedly but were probably related to maintaining balance. The mounting bird then tread on the other bird's back a few times, leaned back, fluttered its wings for stability, and moved its tail under that of the inviting bird's to make cloacal contact, usually for no more than 1–2 sec (Fig. 4H). Normally, the entire copulation sequence was repeated with roles reversed, including reverse mounting. After dismounting, the bird performed the *Post-copulatory Display* (Fig. 4I), walking in a semi-circle around the front of its mate, which remained in the *Invitation Display.* The wings were fanned and vertical, with the leading edge towards the ground. The contour feathers were raised, with the head held low and the neck held the same way as in the *Nest Defense Display.*

Nest Defense Displays (Fig. 3J–K) were directed at any intruder that approached too close to the nest or chicks, except for crabs, which were vigorously pecked. Birds rushed towards the intruder in the *Full Nest Defense*

Display (Fig. 4J) with wings held fully open and vertical, and the leading edge pointing towards the ground. The body was held low and horizontal and the head kept close to the body, facing the intruder while obscuring the throat patch. The undertail coverts were fully fanned. The mantle and back feathers were slightly raised. The displaying bird stopped and walked back and forth ~1 m in front of the intruder. Birds also made rapid attacks with a single, jabbing peck at the intruder. If the intruder didn't advance further, the displaying bird would at times circle the intruder. The intensity of the display decreased quite rapidly and birds adopted the *Partial Nest Defense Display* (Fig. 4K) with both wings partially folded or, more usually, the wing away from the intruder completely folded. This was followed by a *Staring Display* identical to the *Territorial Defense Display* except the contour feathers were completely raised and the displaying bird usually stood still and stared directly at the intruder; the contour feathers were gradually lowered as the display ended. An incubating or brooding bird stayed on the nest until the intruder was within 1 m if a mate was present and displaying. The bird left the nest in the *Full Nest Defense Display* if the intruder came closer, and either charged at the intruder or moved to the side (possibly in an attempt to divert attention from the nest). If an intruder attempted to raid the nest, the incubating bird stood next to or over the nest and attacked the intruder, making powerful, jabbing pecks and giving a loud, piercing squeal that was only given in this context. Birds often followed a retreating intruder, at times in the *Partial Nest Defense Display*. At this ostensibly critical juncture, birds occasionally stopped mid-display to feed; this may have been displacement behavior.

When 'courtship feeding' or provisioning young, a bird with food in its bill approached the intended recipient and adopted the *Provisioning Posture*. The head was pointed vertically downwards so the bill almost touched the ground. The rest of its body was in the *Relaxed Posture*. This posture was maintained until the food item had been taken. If a chick dropped food or struggled to handle it, the adult would pick it up repeatedly, at times breaking the item into smaller pieces. The chick usually approached the adult in this posture from the side and underneath, small chicks even standing under the chest of the adult.

Aggressive and *Submissive Displays* (Fig. 4L) were distinct from the *Territorial Defense Display* and differed from the positions for fighting in that only one bird was aggressive. These displays formed part of intra-pair behavior and were also used when adults evicted young from the natal territory. When a bird performed the *Aggressive Display*, it adopted the *Upright Posture* while approaching another bird. It then stood over the other bird and leaned forward when attacking. The aggressor would also grab the other bird's head or neck in its bill or push the other bird with its chest. The bird being attacked either adopted a *Submissive Posture* or fled. In the *Submissive Posture*, the bird crouched on the ground with its neck retracted and the head pointing down and away from the aggressor, hiding the throat patch. No undertail coverts were visible, the wings were kept folded, and the contour feathers were flattened. We only observed intra-pair aggression arising from direct competition for food outside the breeding season. During the breeding season it appeared to be a pair-bonding behavior, but was also used in competition for food. Where gender of birds in intra-pair aggressive interactions was known, the aggressor was usually male.

DISCUSSION

Aldabra Rails form monogamous pairs that vigorously defend their territories against intruders; both pair bonds and territory boundaries were stable across breeding seasons. Males and females shared duties associated with breeding (e.g., incubation and chick provisioning) and territoriality (e.g., territorial defense). They foraged in all vegetation types on Aldabra but preferred dense mixed scrub (Penny and Diamond 1971, Wanless 2002). They were seldom encountered in monospecific stands of *Casuarina equisetifolia*, possibly reflecting a paucity of understory cover or low invertebrate prey densities (Spaull 1979). They regularly foraged in mangrove (*Rhizophora* sp.) swamps, but vacated these at high tide (Penny and Diamond 1971, this study). In addition to terrestrial arthropods, which dominate the diet, they also eat berries, flower petals, intertidal invertebrates, organic jetsam on

beaches, turtle and tortoise eggs and hatchlings, skinks, geckos, crabs, carrion, and kitchen scraps (Penny and Diamond 1971, Frith 1977, Huxley 1982, this study). Neither this study nor Huxley's (1982) quantified the diet of Aldabra Rails. This was due to the difficulties of observing birds in dense vegetation without disrupting their feeding. Slow-motion replay of video recordings is probably the only way to gather reliable data on feeding ecology.

A significant finding of this study is that gender of Aldabra Rails cannot be reliably ascertained in the field. We incorrectly identified gender of 11 birds that were in the hand at the time and could be closely examined. This casts doubt over interpretations of Aldabra Rail biology and behavior from earlier studies (e.g., Penny and Diamond 1971, Huxley 1982). It also led to the discovery of reverse mounting in the species.

A second finding that refutes published information about Aldabra Rails relates to their territoriality. Penny and Diamond (1971) argued that territories are not necessarily contiguous, but conform to a 'neighborhood' system, where core territories are defended but communal foraging areas exist. Neither Huxley (1982) nor we found any evidence to support this assertion.

Huxley (1979) described a mutualistic relationship between Aldabra Rails and Aldabra giant tortoises (*Dipsochelys dussumieri*). The rails reportedly glean flies, dead skin or ectoparasites from tortoises, which in turn assist by adopting a distinctive posture, exposing the full surface of skin to be gleaned. Neither we nor anyone else with whom we have worked or consulted has witnessed this interaction. On the contrary, Aldabra Rails regularly foraged less than a meter from giant tortoises and neither species showed the slightest interest in the other.

A recent text on the Aldabra Rail (e.g., Sinclair and Langrand 1998) treated it as a distinct species from the White-throated Rail of Madagascar. A taxonomic review based on genetics and vocalizations is presently underway, but a greater understanding of the Aldabra Rail's biology is necessary in understanding its evolution, distinctiveness, conservation status, and threats to its persistence on Aldabra. In addition, there are consistent differences in plumage coloration between birds from Île aux Cèdres versus Malabar and Polymnie islands that merit closer investigation.

The reintroduced population (on Picard) produced clutches of up to four eggs, in contrast to the limited evidence of three-egg clutches being the maximum on Malabar. This suggests the species' maximum clutch size is four. We failed to find second clutches following successful first clutches on Malabar, but at least six pairs on Picard attempted double-brooding. The Aldabra Rail's response to good breeding conditions appears to be to increase reproductive effort by increasing clutch size and clutch frequency. Huxley (1982) reported two repeat clutches from Malabar pairs (no total sample size given). In general, it is likely that replacement clutches will be laid but repeat clutches are expected to be quite rare.

There are three points of particular interest regarding reproductive displays of the rails. One, termed *pseudo-copulation*, involves mounting but excludes cloacal contact. We interpret this as a pair-bonding activity. The second is reverse mounting (where the female mounts the male). This behavior has been reported from a diversity of bird species (James 1983), including rallids (e.g., Anderson 1975, Brooke 1992). Reverse mounting is known to be a regular component of pair bonding/sexual behavior in relatively few bird species (James 1983, Nuechterlein and Storer 1989). Last, the *Post-copulatory Display* was described by Frith (1977) who conjectured that it was restricted to extra-pair copulations—this is not the case.

Aldabra has five species that are potential nest predators: the terrestrial Robber Crab (*Birgus latro*), Malagasy Kestrel (*Falco newtoni*), Malagasy Coucal (*Centropus toulou*), Pied Crow (*Corvus albus*), and black rat (*Rattus rattus*), the latter being an introduced species. The loss of seven eggs (5 of which were individual losses from successful clutches) and 12 of 28 chicks suggests that nest predators are successful in raiding Aldabra Rail nests and in preying on nestlings. However, Aldabra Rails have strong nest and chick defense instincts. First, they do not flush from the nest in the same way as species that have high adult mortality rates at the nest (cf. Conway and Martin 2000, Lloyd 2004). Second,

the hiding behavior of chicks in response to the danger call from parents is strong. Furthermore, no adult Aldabra Rail has ever been reported to be attacked by predators. These data lend support to the hypothesis that eggs and chicks are at risk of predation, but adults are not, or at least much less so, given the absence of other (introduced) predators. We posit that Aldabra Rails have evolved on Aldabra in the absence of predators of adults and lack appropriate behaviors. The *Nest Defense* displays described would be entirely inappropriate for a predator capable of taking adult Aldabra Rails.

The present-day absence of significant predators of adult Aldabra Rails is fortuitous. They are not at risk from black rats (Penny and Diamond 1971; Frith 1977; Huxley 1982; Wanless 2002, 2003b). Rats typically retreat in the face of aggression from Aldabra Rails, which are capable of killing them (Wanless 2003b). The ranges of Aldabra Rails and feral domestic cats (*Felis catus*) do not overlap on Aldabra and cats are thought to be largely responsible for the local extinction of Aldabra Rails on Grande Terre and Picard islands (Wanless 2002). However, local extinctions happened before many interactions were recorded and there are only two records of Aldabra Rails interacting with cats (Huxley 1982, Hambler et al. 1993). In both instances, Aldabra Rails adopted a *Nest* or *Territory Defense Posture* rather than flee. This implies that Aldabra Rails do not have an appropriate (i.e., fleeing) response to cats, and do not treat them as potential predators. The presence of the Norway rat (*Rattus norvegicus*) elsewhere in the Seychelles is a source of concern, as it is bigger and more aggressive than the black rat, and its impacts on insular avifauna are much greater (Towns et al. 2006). We predict that inappropriate responses of Aldabra Rails to cats (and to humans close to their nests) are likely to be similarly maladaptive for other novel predators. Dispersal of cats, Norway rats or other mammalian predators to any of the four islands where the Aldabra Rail now occurs will pose a significant threat to the survival of the species. Quarantine/bio-security procedures that minimize risk of further colonizations should be a priority and put in place for all visits to Aldabra.

ACKNOWLEDGMENTS

Rachel Wiseman and Richard White provided invaluable help in the field. Gabby Raaff produced illustrations of the postures and displays. Jessica Cunningham performed the genetic identification of gender. Some of the descriptive terminology we used to classify and describe postures and displays was originally used by C. R. Huxley. Barry Taylor, John Cooper, J. R. Young and an anonymous referee greatly improved earlier drafts. We received financial and/or logistical support from the Seychelles Islands Foundation, Dutch Trust Fund, Conservation International, and the Center for Applied Biodiversity Science, the (South African) National Research Foundation, and the University of Cape Town.

LITERATURE CITED

Anderson, A. 1975. A method of sexing Moorhens. Wildfowl 26:77–82.

Benson, C. W. 1967. The birds of Aldabra and their status. Atoll Research Bulletin 118:63–111.

Benson, C. W. and M. J. Penny. 1971. The land birds of Aldabra. Philosophical Transactions of the Royal Society of London, B 260:417–527.

Brooke, R. K. 1992. Apparent reverse mounting in the African Rail *Rallus caerulescens*. Ostrich 63:185.

Collar, N. J. 1993. The conservation status in 1982 of the Aldabra White-throated Rail *Dryolimnas cuvieri aldabranus*. Bird Conservation International 3:299–305.

Conway, C. J. and T. E. Martin. 2000. Evolution of avian incubation behavior: influence of food, climate and nest predation. Evolution 54:670–685.

Fridolfsson, A. K. and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30:116–121.

Frith, C. B. 1977. Life history notes on some Aldabra land birds. Atoll Research Bulletin 201:1–15.

Hambler, C., J. M. Newing, and K. Hambler. 1993. Population monitoring for the flightless rail *Dryolimnas cuvieri aldabranus*. Bird Conservation International 3:307–318.

Huxley, C. R. 1979. The tortoise and the rail. Philosophical Transactions of the Royal Society of London, B 286:225–230.

Huxley, C. R. 1982. Unpublished typescript on the Aldabra Rail. Archived in Royal Society of London Library, London, United Kingdom.

James, P. C. 1983. Reverse mounting in the Northwest Crow. Journal of Field Ornithology 54:418–419.

Lloyd, P. 2004. Variation in nest predation among arid-zone birds. Ostrich 75:228–235.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Mourer-Chauviré, C., R. Bour, S. Ribes, and F. Moutou. 1999. The avifauna of Réunion Island (Mascarene Islands) at the time of the arrival of the first Europeans. Pages 1–38 *in* Avian paleontology at the close of the 20th Century: Proceedings of the 4th International Meeting of the So-

ciety of Avian Paleontology and Evolution (S. L. Olson, Editor). Washington, D.C., USA.

Nuechterlein, G. L. and R. W. Storer. 1989. Reverse mounting in grebes. Condor 91:341–346.

Nur, N., A. L. Holmes, and G. R. Geupel. 2004. Use of survival time analysis to analyze nesting success in birds: an example using Loggerhead Shrikes. Condor 106:457–471.

Penny, M. J. and A. W. Diamond. 1971. The White-throated rail, *Dryolimnas cuvieri* on Aldabra. Philosophical Transactions of the Royal Society of London, B 260:529–548.

Rand, A. L. 1936. The distribution and habits of Madagascar birds. Bulletin of the American Museum of Natural History 72:143–499.

Rountree, R. R. G., R. Guérin, S. Pelte, and J. Vinson. 1952. Catalogue of the birds of Mauritius. Mauritius Institute Bulletin 3:155–217.

Sinclair, I. and O. Langrand. 1998. Birds of the Indian Ocean islands. Struik, Cape Town, South Africa.

Spaull, V. W. 1979. Distribution of soil and litter arthropods on Aldabra Atoll. Philosophical Transactions of the Royal Society of London, B 286: 109–117.

Starck, J. M. and R. E. Ricklefs. 1998. Patterns of development: the altricial-precocial spectrum. Pages 3–30 *in* Avian growth and development (J. M. Starck and R. E. Ricklefs, Editors). Oxford University Press, New York, USA.

Stoddart, D. R. 1971. Rainfall on Indian Ocean coral islands. Atoll Research Bulletin 147:1–21.

Taylor, B. and B. van Perlo. 1998. Rails: a guide to the rails, crakes, gallinules and coots of the world. Pica Press, Sussex, United Kingdom.

Towns, D. R., I. A. E. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8:863–891.

Wanless, R. M. 2002. The reintroduction of the Aldabra Rail *Dryolimnas cuvieri aldabranus* to Picard Island, Aldabra Atoll. Thesis. University of Cape Town, South Africa.

Wanless, R. M. 2003a. Can the Aldabra White-Throated Rail *Dryolimnas cuvieri aldabranus* fly? Atoll Research Bulletin 508:1–7.

Wanless, R. M. 2003b. Flightless Aldabra Rail *Dryolimnas cuvieri aldabranus* kills black rat *Rattus rattus*. Ostrich 74:134.

Wanless, R. M., J. Cunningham, P. A. R. Hockey, J. Wanless, R. W. White, and R. Wiseman. 2002. The success of a soft-release reintroduction of the flightless Aldabra Rail (*Dryolimnas* [*cuvieri*] *aldabranus*) on Aldabra Atoll, Seychelles. Biological Conservation 107:203–210.

The Wilson Journal of Ornithology 120(1):62–73, 2008

POST-FLEDGING MOVEMENT AND SPATIAL HABITAT-USE PATTERNS OF JUVENILE SWAINSON'S THRUSHES

JENNIFER D. WHITE[1,2,3] AND JOHN FAABORG[1]

ABSTRACT.—We used radio telemetry to study post-fledging dispersal patterns of juvenile Swainson's Thrushes (*Catharus ustulatus*) in central coastal California from 2000 to 2002. We followed 30 different broods during the dependent period and 35 juveniles after independence. Adults with dependent juveniles had two types of movements, drifting and stationary, similar to those described for Wood Thrush (*Hylocichla mustelina*). All juveniles established at least one post-fledging dispersal area (n = 29) after independence and most (62%) established a second; therefore, most home ranges were comprised of disjunct dispersal areas. Median home range (95% fixed-kernel) and core (50% fixed-kernel) areas were 2.0 ha (range = 0.2–9.0) and 0.41 ha (range = 0.05–1.6), respectively. Juveniles spent from 3 to 39 days in different post-fledging dispersal areas; they generally had a primary dispersal area where they spent the majority of their time. Juveniles spent an average of 22.7 ± 1.5 days in primary and 9.6 ± 0.9 days in secondary dispersal areas. The median post-fledging dispersal distance was 147 m (range = 28–1,040 m) for initial dispersal from a brood-rearing area and 418 m (range = 154–2,624 m) for subsequent dispersal movements. Initial dispersal was not directed; however, final dispersal (brood-rearing area to final location) was directed to the northwest for all plots combined and west for one plot. We suggest that post-fledging movements and spatial habitat-use patterns are affected by adult breeding strategies, and by spatially and temporally clumped resources. *Received 2 October 2006. Accepted 17 July 2007.*

Post-nesting movements and spatial habitat-use patterns may reveal important aspects of post-fledging ecology for juveniles and post-breeding ecology for adults; however, little information exists on movements and spatial patterns of juvenile birds. This is largely because juveniles are non-territorial and cryptic and, therefore, difficult to follow as they disperse from the natal area. Post-fledging movement patterns have only been described for a few passerine species including Wood Thrush (*Hylocichla mustelina*) (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002, Fink 2003), White-throated Thrush (*Turdus assimilis*) (Cohen and Lindell 2004), Lark Bunting (*Calamospiza melanocorys*) (Yackel Adams et al. 2001), Ovenbird (*Seiurus aurocapillus*) (Bayne and Hobson 2001), Hooded Warbler (*Wilsonia citrina*) (Rush 2003), Dickcissel (*Spiza americana*) (Berkeley et al. 2007, Suedkamp Wells et al. 2008), and Eastern Meadowlark (*Sturnella magna*) (Kershner et al. 2004, Suedkamp Wells et al. 2008).

Studies of movements during the post-fledging dependent period, when juveniles are still with their parents, have shown that adults may have two types of movement patterns, one where adults stay on the breeding territory during the post-fledging period (stationary movements) and another where adults move from the breeding territory (drifting movements) (Anders et al. 1998, Vega Rivera et al. 2000). Vega Rivera et al. (2000) considered these movements (remaining on or moving from the breeding territory) to be different adult strategies, and the strategy used depended on whether the adult had completed breeding activities and on where it wanted to molt. Adults also may split broods during the dependent period with males and females each caring for different fledglings (Green and Cockburn 2001, Yackel Adams et al. 2001), and the distances that dependent fledglings move may vary depending on whether the attending parent is male or female (Rush 2003). Movements during the dependent period also may vary depending on whether the adult is in a fragmented or contiguous forest (Rush 2003), and males with young may not move as far or be as likely to cross gaps as males without young (Bayne and Hobson 2001).

There is little information on post-fledging movements of juvenile passerines after independence from their parents. However, studies of independent Wood Thrush juveniles demonstrated that juveniles used vegetation types

[1] Division of Biological Sciences, 110 Tucker Hall, University of Missouri, Columbia, MO 65211, USA.

[2] Current address: Puerto Rico Conservation Foundation, c/o International Institute of Tropical Forestry, USDA, Forest Service, Sabana Field Research Station, HC 02 Box 6205, Luquillo, Puerto Rico 00773, USA.

[3] Corresponding author;
e-mail: jend.white@gmail.com

different from those used by breeding adults (Anders et al. 1998, Vega Rivera et al. 1998, Fink 2003), made exploratory movements (Vega Rivera et al. 1998), moved in a southerly direction (Anders et al. 1998), congregated in conspecific and mixed-species flocks (Vega Rivera et al. 1998, Fink 2003), remained solitary (Anders et al. 1998, Lang et al. 2002), and had from one to as many as five distinct post-fledging dispersal areas (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002, Fink 2003). However, movement and spatial use patterns described for Wood Thrush may not be relevant to other species, vegetation types, landscapes, or regions.

We describe post-fledging movements and dispersal for Swainson's Thrushes (*Catharus ustulatus*) in a western habitat mosaic of riparian forest, coastal scrub, mixed-hardwood forest, and grazed and ungrazed annual grasslands. The study subspecies (*C. u. oedicus*) is endemic to California; this subspecies nests in shrubs and is unique among Swainson's Thrushes in that it breeds primarily in riparian forests rather than coniferous forests. Swainson's Thrushes are insectivore/frugivores (Evans Mack and Wang 2000) and foraging patches with abundant fruit were shown to be important to juvenile resource selection (White et al. 2005). The objectives of our study were to: (1) describe movements of adults with dependent broods, (2) describe dispersal of juveniles after they become independent from their parents, and (3) estimate juvenile home range size during the post-fledging period.

METHODS

Study Area.—We studied Swainson's Thrushes in riparian forests along three creeks in Marin County, California: Redwood Creek (37° 51′ N, 122° 34′ W, Muir Woods National Monument), Lagunitas Creek (38° 02′ N, 122° 45′ W, Golden Gate National Recreation Area), and Muddy Hollow (38° 02′ N, 122° 52′ W, Point Reyes National Seashore). Riparian vegetation was typical of central coastal California and was primarily red alder (*Alnus rubra*) and arroyo willow (*Salix lasiolepis*). The adjacent vegetation types at each creek were coastal scrub (Muddy Hollow and Redwood Creek), mixed-hardwood forest (Lagunitas and Redwood creeks), Bishop pine (*Pinus muricata*) forest (Muddy Hollow), and grazed (Lagunitas Creek) and ungrazed (Muddy Hollow and Redwood Creek) annual grasses.

Field Methods.—We used radio telemetry to study post-fledging movements of juvenile Swainson's Thrush from 2000 to 2002. We searched for and monitored nests following standardized protocols (Martin and Geupel 1993) on pre-existing nest plots established by PRBO Conservation Science (PRBO). There were two nest plots along each creek. Nest plots at Redwood Creek were 1,400 m apart and plots A and B were 4.9 and 4.2 ha, respectively. Nest plots at Lagunitas Creek were 640 m apart and plots A and B were ~7.4 and 3.9 ha, respectively. Nest plots at Muddy Hollow were 500 m apart and plots A and B were 8.3 and 3.1 ha, respectively. We did not survey Muddy Hollow for nesting activity due to time constraints after 2000. Each nest plot at Redwood and Lagunitas creeks had an average of 21 Swainson's Thrush territories each year from 2000 to 2002 (J. D. White, unpubl. data). We banded nestlings on days 9 and 10 of the nestling period; each nestling received a USGS aluminum band and a unique combination of three color-bands.

At least one (rarely up to 3) nestling per brood was fitted with a radio transmitter using the leg-harness method (Rappole and Tipton 1991). We used a harness made of cotton covered elastic string with adjustable leg loops that were attached to the transmitter prior to placement on nestlings in the field. This allowed for quick adjustment of harness length and attachment in the field. We used 1.4-g transmitters during 2000 with an average life of 60 days (Advanced Telemetry Systems [ATS], Itasca, MN, USA). We used refurbished ATS transmitters and new 1.1-g transmitters during 2001 with an average life of 50 days (Holohil Systems Ltd. Ottawa, ON, Canada). Transmitters weighed 4% (2000) and 3% (2001–2002) of average adult thrush body mass (30 g). We used hand-held receivers (model R-1000) and Yagi three-element directional antennas (model RA-150, Communications Specialists, Inc. Orange, CA, USA) to locate radio-marked individuals.

We located juveniles once every 2 to 4 days after fledging until independence. We checked juveniles after independence every other day,

homing in on the animal to estimate its location (White and Garrott 1990). We attempted to visually relocate juveniles; when we were unable to observe a juvenile we circled the individual within a 10–20 m radius. We were able to correctly identify the vegetation type the juvenile was using by standing at the edge of two vegetation types and plotting juvenile location. We marked two GPS locations per day, for a total of 20–30 locations per bird, using the Universal Transverse Mercator (UTM) grid system. We used a handheld Garmin GPS unit (GPS II Plus) and only recorded points with a low estimate of error (Figure of Merit [FOM] <10). We alternated checks of individuals between morning and afternoon on subsequent visits to ensure that each bird was monitored during different time periods throughout the day. Twice-daily locations were separated by 2 hrs to ensure the juvenile had sufficient time to move if it desired (Pasinelli et al. 2001) and to guard against autocorrelation of points (Otis and White 1999). We monitored juveniles for 15 to 30 min and recorded behavior, food items taken, and presence of conspecifics or other avian species. We used this information to ascertain if juveniles were with parents and siblings, and whether they were foraging independently.

Juveniles that left the natal area without returning and were no longer observed with parents or siblings were considered biologically independent. Swainson's Thrush juveniles after biological independence from siblings and parents, are expected to be statistically and spatially independent and to disperse independently from each other as was reported for Wood Thrush (Anders et al. 1998, Vega Rivera et al. 1998). Siblings were considered spatially independent as long as their locations did not track each other in space or time (Erickson et al. 2001). We plotted locations of biologically independent siblings in ArcView GIS (ESRI 2000) to visually examine if sibling locations tracked each other; in no instance did siblings or non-related individuals track each other in space and time.

Analyses.—We projected juvenile locations onto aerial photographs in ArcView to study movements of adults with dependent broods (movements from when juveniles leave the nest until they become biologically independent from their parents). We considered any location where a juvenile was attended by an adult to be a "dependent–period" location and, therefore, a brood-rearing location. We calculated and plotted the center of all brood-rearing locations, and measured the distance from the nest to the center of the brood-rearing area, which is defined as the area where adults raise their young; these areas can be close to or far from the nest. We measured nest to brood-rearing area in one case separately for two juveniles from the same brood because they were 17 m apart. Broods reared within the natal area (≤50 m of the nest) were considered stationary and broods reared outside the natal area (>50 m from the nest) were considered drifting. We chose 50 m to separate brood types because stationary brood types were within 50 m of the nest. We wanted to quantify differences between the two brood rearing strategies (stationary and drifting) and examine whether differences in dependent period movements resulted in differences in independent period movements. We used non-parametric one-way ANOVA (PROC NPAR1WAY) to examine whether mean distance moved from nest to brood-rearing area, and mean initial and subsequent dispersal distances differed by stationary or drifting natal movements (SAS Institute 1999). We separated nests into early versus late nests and used Fisher's exact test to examine if there were differences by brood type (early vs. late fledging) (SAS Institute 1999). We considered nests initiated on or before 15 June early nests and those initiated after this date late nests. This date (15 Jun) was the median date of egg laying for Swainson's Thrushes during the study and first fledglings of the year fledge during early June (J. D. White, unpubl. data).

We measured mobility (m/day) for each individual by estimating daily movements from calculations of the distance between subsequent locations (Batschelet 1981) and divided that distance by the number of days between relocations (Forsman et al. 2002). We calculated median mobility by age group, and by drifting and stationary brood movements.

Post-fledging dispersal is the movement of an independent juvenile from the natal area, or from parents and siblings in a brood-rearing area (Anders et al. 1998). Post-fledging dispersal differs from natal dispersal, which is the movement of a bird from where it hatched

to its first breeding site (Greenwood 1980). We considered post-fledging dispersal to have started either when juveniles left the natal area on their own without returning, or when birds dispersed from a brood-rearing area and were no longer associating with their parents or siblings. We did not use a minimum distance moved as a criterion to define the onset of post-fledging dispersal because a juvenile could move a short distance and be outside the natal area.

We defined initial dispersal as the distance from the center of the brood-rearing area to the center of the first post-dispersal area. We defined subsequent dispersal as the distance between the centers of different post-dispersal areas (e.g., first, second, third, etc.). We considered a post-dispersal area distinct if a bird stayed in the area for ≥3 days. Juveniles may have more than one area of concentrated use within one post-dispersal area; we refer to these as multiple centers of activity. We measured initial and subsequent dispersal distances and the distance between multiple centers of activity using the distance measurement tool in the Animal Movements extension in ArcView (Hooge and Eichenlaub 1997).

We calculated direction traveled from the center of the brood-rearing area to the first post-fledging dispersal area (initial dispersal direction) and to the final location (final dispersal direction) for each bird (Batschelet 1981, Kernohan et al. 2001). We used the Rayleigh test to examine if the initial or final dispersal directions were random or oriented (Batschelet 1981). We tested for orientation at Redwood Creek (by plot), at Lagunitas Creek (both plots combined, due to smaller sample size), and at both creeks combined.

We quantified two other types of movements, exploratory and wandering movements. An exploratory movement was defined as a movement greater than 300 m from an established dispersal area and subsequent return to that area. Wandering movements were defined as locations where a bird stayed for <3 days in between established dispersal areas.

We calculated home ranges for individual Swainson's Thrush juveniles with at least 25 locations (Seaman et al. 1999). A home range is defined as the extent of area with a defined probability of occurrence of an animal during a specified time period (Kernohan et al. 2001). We considered all post-fledging juvenile locations (dependent and independent) to be a part of their post-fledging home range.

Kernel methods are recommended over other methods for home range estimation with small sample sizes (Kernohan et al. 2001). We used program KERNELHR (Seaman et al. 1998) to estimate home range areas; this program calculates volume percentages which estimate the true use distribution (UD) rather than point percentages which only give estimates of UD. KERNELHR also calculates smoothing parameters separately for the x and y dimensions, allowing the kernel to better fit linear geographic features (e.g., rivers and mountain canyons).

We used the fixed-kernel with the Least Squares Cross Validation smoothing parameter (h-LSCV) to estimate home range (95% fixed-kernel) and areas of concentrated use or core areas (50% fixed-kernel). While there are limitations to h-LSCV smoothing (Horne and Garton 2006) it is generally recommended over reference smoothing options available in software programs (Kernohan et al. 2001). The smoothing parameter failed (h-LSCV went to zero) for eight juveniles due to tightly clustered locations. We moved clustered or duplicate locations slightly (1 or 2 m) for five of these individuals which corrected smoothing parameter failures. We deleted all but one or two of the clustered locations to correct smoothing parameter failures for another three individuals, and used KERNELHR with the reduced data set to obtain smoothing parameter values ($h_{(x)}$ and $h_{(y)}$), and then used KERNELHR with the full data set using these values. Results are reported as means ± SE unless otherwise indicated.

RESULTS

We color banded 178 Swainson's Thrush nestlings from 62 nests. Sixty-seven nestlings were radiomarked from 61 nests (18 nestlings in 2000, 32 in 2001, and 17 in 2002) from which 35 juveniles reached independence from 30 different nests. We followed 10, 12, and 13 juveniles to independence in 2000, 2001, and 2002, respectively.

Immediately after fledging, juveniles used thicket areas near the nest. Thickets could be tall shrubs (e.g., arroyo willow or red elder-

TABLE 1. Distances (m) moved for Swainson's Thrush broods with stationary and drifting dependent period movements and for independent juveniles, Marin County, California, 2000–2002.

Movement type	*n*	Mean	SE	Median	Range
Stationary, nest to brood-rearing area	22	28	2	30	9–49
Drifting, nest to brood-rearing area	9	189	102	70	25–994
Initial dispersal distance	34	242	41	147	28–1,040
Subsequent dispersal distance	28	598	101	418	154–2,624
Exploratory movement	11	439	31	422	289–651

berry [*Sambucus racemosa*]) or trees with low lying branches (e.g., red alder or boxelder [*Acer negundo*]) that reached into herbaceous cover, where fledglings remained close to the ground. Brood-rearing areas were in riparian, mixed-hardwood forest, and coastal scrub vegetation types.

Five juveniles (14%) used only riparian vegetation after post-fledging dispersal, three (9%) used only upland vegetation types (coastal scrub or mixed-hardwood forest), and 27 (77%) used both riparian and adjacent upland vegetation types.

Brood Movements.—Swainson's Thrush adults had both stationary (n = 21 broods) and drifting movements (n = 9 broods) during the post-fledging dependent period (Table 1, Fig. 1). The proportion of drifting broods was the same among early (30%) and late (27%) nests (P = 1.0, two-tailed Fisher's exact test). Mobility was low for the first few days post-fledging for both movement types (Table 2). Mobility increased for drifting broods during days 3 to 7 post-fledging and again during days 8 to 12 post-fledging. Drifting adults led fledglings to brood-rearing areas that were on average 150 m farther from the nest than stationary broods (F = 6.31, df = 1, $P < 0.02$; Table 1). Although drifting adults led young birds hundreds of meters from the natal area, the maximum daily distance moved was about 40 m/day (Table 2, Fig. 1). Median mobility was 3 to 12 m/day greater for drifting broods than stationary broods during the first 12 days after fledging (Table 2). Mobility increased for stationary juveniles during days 8 to 12 and 13 to 19 after fledging when these juveniles began dispersing independently.

Brood-rearing areas used by drifting adults in 8 of 9 cases, consisted of fruiting shrub thickets with abundant fruit (twinberry [*Lonicera involucrata*], Himalayan blackberry [*Rubus discolor*], and dogwood [*Cornus sercia*]); in the other case, there were abundant oak moths (*Phryganidia californica*) in the brood-rearing area. Adults led juveniles on three occasions to areas identified as "population-level core areas". Population-level core areas were areas that contained abundant fruit and were used by more than one radio-marked thrush each year, and were used during each year of the study. Adults on one occasion also led a juvenile across an old field gap of 78 m between the riparian natal area to coastal scrub foraging area; the fledgling had been out of the nest for 10 days.

Juveniles from drifting broods spent an average of 8.6 fewer days in the natal area than stationary broods (Fig. 2A); however, they stayed with parents and siblings 5 days longer (Fig. 2B, C) on average. Two siblings in one case dispersed from the natal area at different ages, one at 15 and the other at 22 days post-fledging.

Spatial Use Patterns and Home Range Estimates.—All Swainson's Thrushes after independence established at least one post-fledging dispersal area (n = 29), 18 individuals (62%) established a second, three individuals (10%) established a third, and one established a fourth. Therefore, the home range for most juveniles was comprised of disjunct dispersal areas. The median home range area (95% fixed-kernel) was 2.0 ha (range = 0.2–9.0, mean [± SE] = 2.58 ± 0.52 ha) and the median core area (50% fixed-kernel) was 0.41 ha (range = 0.05–1.6, mean = 0.49 ± 0.09 ha). The mean number of locations used to estimate individual home ranges was 33 (range = 25–47).

Time spent in different post-fledging dispersal areas ranged from 3 to 39 days. Juveniles generally established a primary dispersal area where they spent most of their time; this

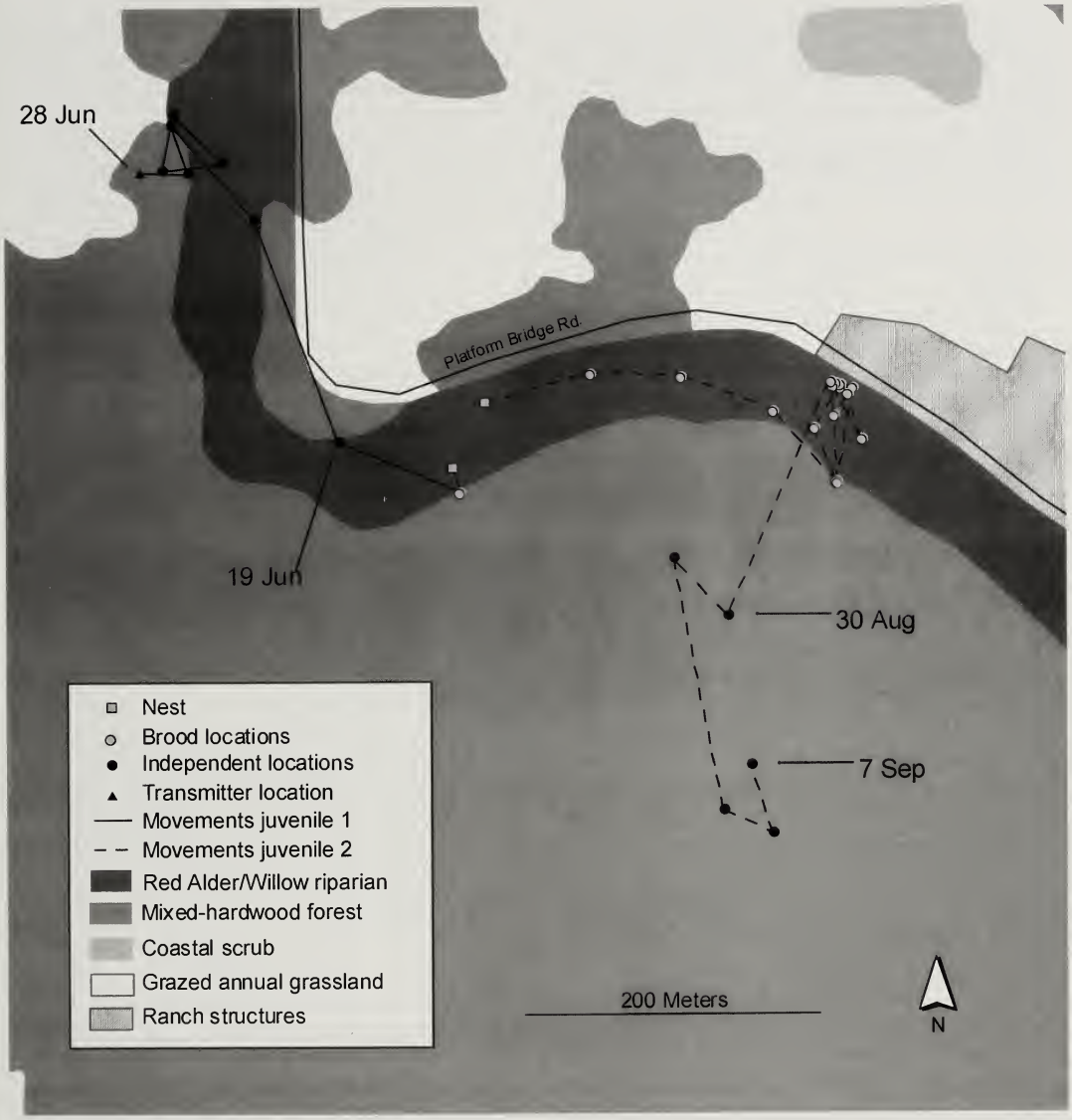


FIG. 1. Nest site, brood, and independent juvenile locations of two juvenile Swainson's Thrushes at Lagunitas Creek, Marin County, California, 2000. The juvenile on the left had stationary brood movements; the juvenile on the right had drifting brood movements.

could be either the first or subsequent dispersal areas. The mean (± SE) number of days spent in the primary dispersal area was 22.7 ± 1.5 days (n = 29, median = 24, range = 6–39) and the mean number of days in the secondary dispersal area was 9.6 ± 0.9 days (n = 18, median = 10, range = 3–15). Two juveniles had two centers of activity within one dispersal area, and both juveniles traveled between these centers daily (Fig. 3). The distance between centers was 231 m and 131 m.

Mobility.—Mobility ranged from a low near zero for all age groups to highs in the hundreds of meters for age groups past 8 days post-fledging (Table 2). Mobility varied greatly because, within a dispersal area, birds generally did not move far, often remaining in the same shrub thicket; however, they made long-distance movements between dispersal areas.

Distance and Direction.—Dispersal distances of independent juveniles did not differ between stationary or drifting natal move-

TABLE 2. Median mobility (m/day) for Swainson's Thrush juveniles with stationary (n = 25) and drifting (n = 12) natal movements, and for all independent juveniles pooled after post-fledging day 20, Marin County, California, 2000–2002. Sample size (n) refers to the number of movements by juveniles in each age group.

Days post-fledging	Stationary		Drifting	
	Mobility (n)	Range	Range	Mobility (n)
0–2	4.5 (30)	0.0–24.2	7.9 (20)	0.5–40.0
3–7	5.9 (38)	0.5–101.5	14.9 (22)	0.0–38.9
8–12	14.1 (59)	1.0–756.7	25.7 (23)	0.5–206.9
13–19	28.9 (114)	0.0–211.8	22.6 (48)	1.0–218.9
20–29	25.5 (236)	0.5–880.3		
30–39	37.0 (178)	0.3–724.6		
40–49	39.6 (124)	0.0–475.9		
≥50	103.9 (38)	2.1–393.1		

ments (initial dispersal, F = 0.03, df = 1, P = 0.86; subsequent dispersal, F = 0.08, df = 1, P = 0.78) so these data were pooled. Most initial dispersal distances were <300 m from the natal area and most subsequent dispersal distances were >200 m (Fig. 4). The average initial dispersal distance was 242 m and average subsequent dispersal distances were 598 m (Table 1). The greatest distance a Swainson's Thrush juvenile traveled between dispersal areas was 2,624 m.

Initial post-fledging dispersal direction was not oriented significantly at Redwood Creek (plots A and B), Lagunitas Creek, or both creeks combined (Table 3). However, initial dispersal at Redwood Creek plot B tended toward a southwest direction (P = 0.05, Table 3); the angular deviation (a measure of dispersion) was relatively small (s = 54°) and the vector length (a measure of concentration around the mean direction, where 0 is not directed and 1 is perfectly directed) was relatively large (r = 0.55, Table 3). Final dispersal was oriented to the west for Redwood Creek plot B and northwest for both creeks combined (Table 3). However, final dispersal direction for both creeks combined may have been an artifact of the strong orientation at Redwood Creek plot B or due to a large sample size. The relatively large angular deviation (s = 64°) and small vector length (r = 0.37) for final dispersal for both creeks indicate that with a smaller sample, this result would not be significant (Table 3).

Wandering and Exploratory Movements.—Eleven individuals had wandering locations of 1–2 days duration. The majority of juveniles wandered after dispersal from the natal area and prior to settling into a first post-fledging dispersal area (64%, n = 7). The remaining juveniles wandered before settling into a second post-fledging dispersal area (36%, n = 4).

Nine juveniles made exploratory movements (e.g., Fig. 4) and one individual made three different exploratory movements. The average distance of exploratory movements was 439 ± 31 m (Table 1). The juvenile in two cases (18%) subsequently returned to the exploratory site and remained there for a longer period of time. Two additional juveniles made movements that were functionally exploratory but were less than 300 m; one of these returned to the exploratory site for its second dispersal area.

DISCUSSION

Juvenile Swainson's Thrushes were generally near the nest and took cover in thicket areas within a day or two post-fledging. Mobility was low for the first few days after fledging, as has been found for recent fledglings in other studies (Vega Rivera et al. 2000, Yackel Adams et al. 2001).

Swainson's Thrush adults with dependent broods had both stationary and drifting modes of movement similar to those described for Wood Thrush (Anders et al. 1998, Vega Rivera et al. 2000). The type of movement chosen may have depended on whether the adults attempted a second brood or whether they had completed breeding activities and moved to a foraging or molting site (Vega Rivera et al. 2000). Swainson's Thrush adults that made drifting movements led fledglings to areas with abundant fruit; these adults were not limited to riparian vegetation and were able to

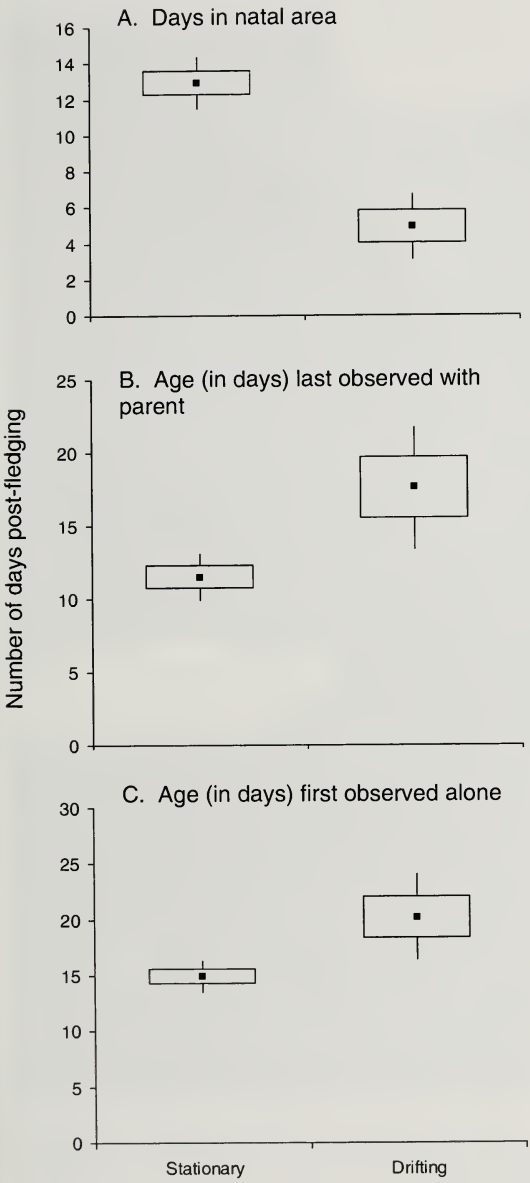


FIG. 2. (A) Mean number of days juvenile Swainson's Thrushes spent on the natal territory or with parents and siblings, (B) age (days post-fledging) last observed with parents, and (C) age at first observation of independence by dependent movement type, stationary (n = 22) or drifting (n = 9), Marin County, California, 2000 to 2002. Mean ± SE and 95% confidence intervals are shown for each box plot.

cross old field gaps to foraging sites. Broods did not appear to be as restricted to forest sites as has been described for some birds in forest fragments (Bayne and Hobson 2001); however, this may not hold true in isolated riparian areas.

Adults were site faithful not only to territories and nest sites but also to brood-rearing sites, leading fledglings to the same areas in subsequent years. Therefore, brood-rearing areas may have an important role in territory or nest-site selection.

Swainson's Thrush fledglings from drifting broods became independent at 20 days post-fledging on average. This age was similar to the average age at dispersal and presumably independence for Wood Thrush (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002, Fink 2003). However, the average age at independence for Swainson's Thrush fledglings from stationary broods was 15 days post-fledging.

The average initial (242 m) and subsequent (598 m) post-fledging dispersal distances for Swainson's Thrushes were less than average dispersal distances reported for Wood Thrush (2.1 km, 1.5 km, 2.2 km, and 825 m, respectively) (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002, Fink 2003). Juvenile Swainson's Thrush may not have had to disperse great distances because of abundant nearby resources (White et al. 2005). The riparian areas in which Swainson's Thrushes bred were narrow and bordered by coastal scrub, which had areas of abundant fruit. Riparian forests also were bordered by mixed-hardwood forest that had oak moth caterpillar outbreaks during late summer and could also have patches of abundant fruit (White et al. 2005). Juvenile Wood Thrushes from fragmented forests in northern Missouri (Fink 2003) also did not disperse as far as juvenile Wood Thrushes from more contiguous forests (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002). Fink (2003) attributed this to nearby second growth or edge in forest fragments, which offered either abundant cover or food; another explanation was that juveniles might be constrained to forest fragments by the surrounding agricultural matrix. However, similar to Swainson's Thrush broods, independent juvenile Swainson's Thrushes were not restricted to riparian forests and readily used adjacent coastal scrub and mixed-hardwood forest.

Southerly movements after fledging may indicate migratory movements (Anders et al.

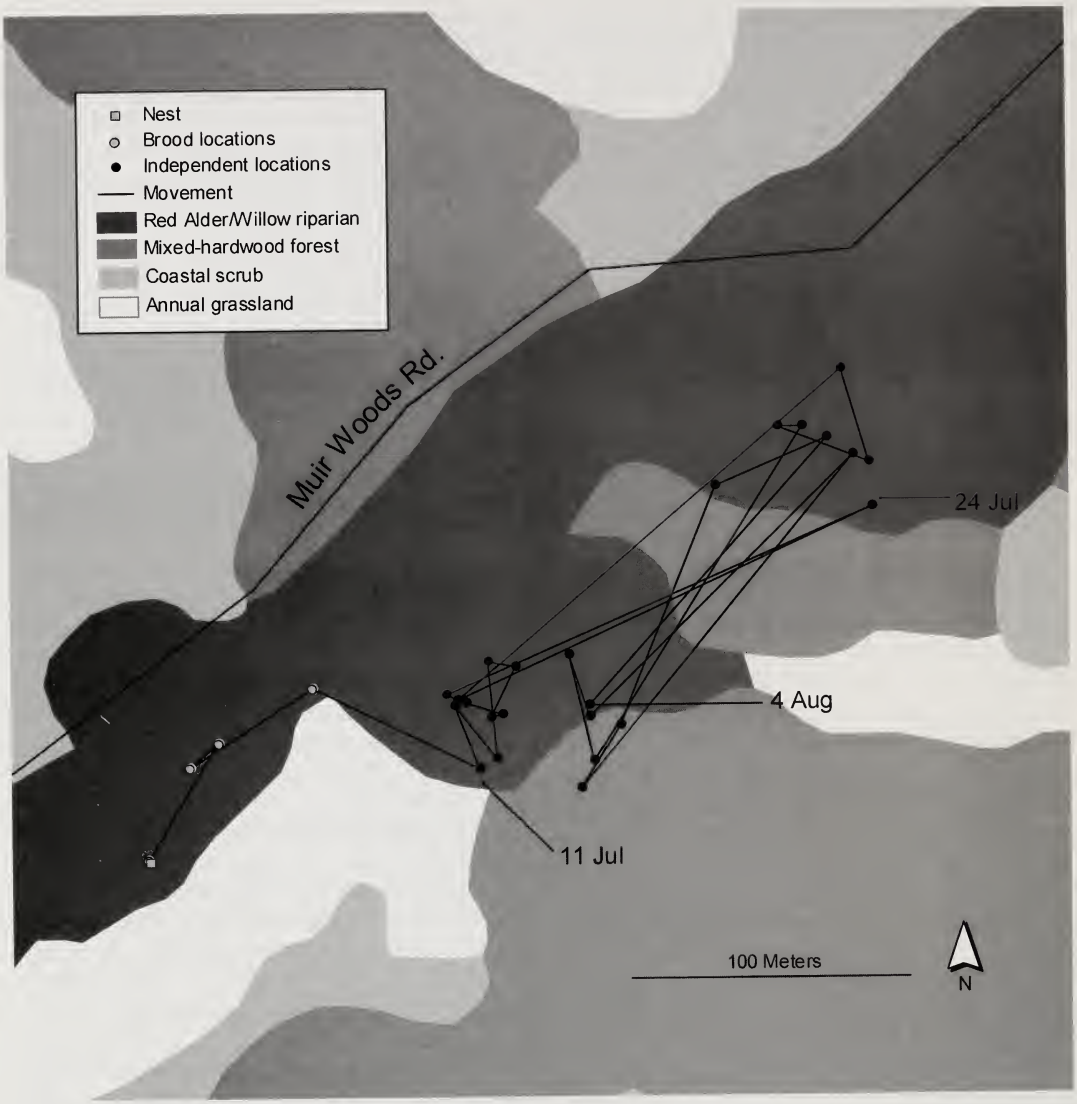


FIG. 3. Nest site, brood, and independent juvenile locations for a juvenile Swainson's Thrush at Redwood Creek, Marin County, California, 2002. This juvenile had two dispersal sites, one of which had two centers of activity. An exploratory movement is indicated by the date, 24 July.

1998); however, three studies of post-fledging Wood Thrushes did not find evidence for southerly movements (Vega Rivera et al. 1998, Lang et al. 2002, Fink 2003). Swainson's Thrush post-fledging dispersal was not generally oriented; however, there was clear evidence for westerly orientation at one plot along Redwood Creek. Therefore, migration likely was not driving movements of Swainson's Thrush juveniles during the post-fledging period (10 Jun–10 Sep). Rather, optimal foraging likely was a more important factor affecting post-fledging independent movements, including the westerly movements at Redwood Creek where birds moved into coastal scrub and areas with abundant ripe fruits (White et al. 2005).

Some Swainson's Thrush juveniles wandered prior to establishing a post-fledging dispersal area, while others also made wandering movements between different dispersal areas. Wandering movements prior to settling and

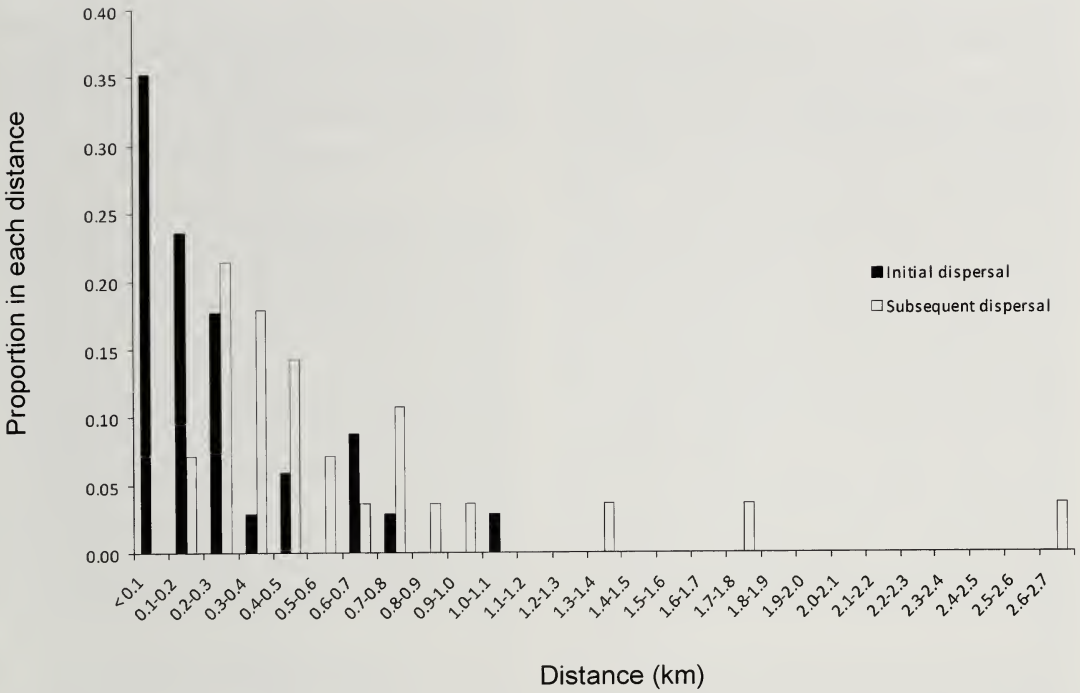


FIG. 4. Proportion of Swainson's Thrush juveniles dispersing by distance category from natal to first post-fledging dispersal area (n = 34), and between subsequent post-fledging dispersal areas (n = 26), Marin County, California, 2000–2002.

between dispersal sites have also been described for Wood Thrush (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002, Fink 2003). Juvenile Swainson's Thrushes also made exploratory movements from their dispersal areas; however, few exploratory movements resulted in resettlement at the exploratory site. Exploratory movements may be important in gaining a sense of location and in searching for new foraging patches (Baker 1982).

Swainson's Thrush home-range estimates (2 ha) were similar to those of juvenile Wood Thrush (average = 2.8 ± 0.5 ha for one dispersal site [Vega Rivera et al. 1998] and 1.5 ± 1.6 ha for first dispersal sites [Anders et al.

TABLE 3. Initial and final post-fledging dispersal direction of Swainson's Thrush juveniles at Lagunitas Creek and at two sites at Redwood Creek, Marin County, California, 2000–2002. Number of juveniles followed at each site (n), mean bearing from true north (b), mean angle (a), and mean angular deviation (s) in degrees, mean vector length (r), and Rayleigh test P-values.

	n	b	a	s	r	P
Initial dispersal						
Lagunitas Creek	11	75	15	74	0.16	0.763
Redwood Creek, A	10	330	120	63	0.39	0.241
Redwood Creek, B	10	230	220	54	0.55	0.050
Creeks combined	33	273	177	74	0.17	0.468
Final dispersal						
Lagunitas Creek	11	307	143	68	0.30	0.380
Redwood Creek, A	10	324	126	61	0.43	0.173
Redwood Creek, B	10	275	175	51	0.61	0.023
Creeks combined	33	297	153	64	0.37	0.019

1998]). Juvenile home ranges were comprised of disjunct dispersal areas and multiple centers of activity, likely due to spatially and temporally clumped resources. The availability of fruit varied in both space and time, depending on fruiting phenology and ecology of different fruiting-shrub species (J. D. White, unpubl. data). Oak moth caterpillars upon which thrushes fed also were patchily distributed in space and time. These caterpillars reached outbreak proportions in mid August and September, and specialized on coast live oak (*Quercus agrifolia*) and California bay (*Umbellularia californica*) trees primarily in mixed-hardwood forest. Home-range estimates were relatively small and used sites often were far apart. For conservation purposes managers may need to preserve large areas that encompass widely dispersed patches of appropriate foraging sites to ensure that resources are available for the post-fledging period.

Swainson's Thrush spatial use patterns were similar to those described for Wood Thrush, despite these species occupying different vegetation types. This is likely due to the similar ecology of these closely related species. Both are insectivore/frugivores that use fruiting shrub thickets during the post-fledging period. Wood Thrushes breed in mature eastern deciduous forest but juveniles sought areas of second growth during the post-fledging period, likely due to abundant fruit resources and cover in these areas (Anders et al. 1998, Vega Rivera et al. 1998, Fink 2003). Home ranges comprised of disjunct areas have also been described for Common Ravens (*Corvus corax*; Roth et al. 2004) and Eurasian Jay (*Garrulus glandarius*; Rolando 1998) that use concentrated and patchily distributed resources. Only one Swainson's Thrush had nest-centered movements as described for Dickcissels (Suedkamp Wells et al. 2008) and Burrowing Owls (*Athene cunicularia*; Davies and Restani 2006).

Research is needed on post-fledging movements and spatial habitat-use patterns in other species, particularly species that presumably rely on a more evenly distributed resource base, to learn if patterns described for Swainson's Thrush and Wood Thrush are general. It will also be important to study these patterns in other vegetation and landscape types to learn how juveniles use space, and the ease with which they can disperse from natal areas and find food and cover during this critical period in the annual cycle.

ACKNOWLEDGMENTS

The Avian Ecology Group at the University of Missouri and two anonymous reviewers made helpful comments on this manuscript. We thank the Golden Gate National Recreation Area (especially Daphne Hatch) and the Point Reyes National Seashore (especially Sarah Allen) for ongoing support of bird monitoring and research. We are grateful for the general support of PRBO, especially Geoffrey Geupel, Nils Warnock, and Thomas Gardali. We also thank PRBO's Terrestrial Ecology Division field crew, especially Roy Churchwell, Jill Harley, Chris Rintoul, and Viola Toniolo for help in the field. This project was funded by a GAANN fellowship, University of Missouri-Columbia, Canon National Parks Science Scholars Program, the National Park Service, National Park Service Fee Demonstration Project, and the Marin Audubon Society.

LITERATURE CITED

Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk 115:349–358.

Baker, R. R. 1982. Migration: paths through time and space. Holmes and Meier Publishers, Inc., New York, USA.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, New York, USA.

Bayne, E. M. and K. A. Hobson. 2001. Movement patterns of adult male Ovenbirds during the postfledging period in fragmented and forested boreal landscapes. Condor 103:343–351.

Berkeley, L. I., J. P. McCarty, and L. L. Wolfenbarger. 2007. Postfledging survival and movement in Dickcisssels (*Spiza americana*): implications for habitat management and conservation. Auk 124:396–409.

Cohen, E. B. and C. A. Lindell. 2004. Survival, habitat use and movements of fledgling White-throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. Auk 121:404–414.

Davies, J. M. and M. Restani. 2006. Survival and movements of juvenile Burrowing Owls during the postfledging period. Condor 108:282–291.

Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. Pages 209–242 *in* Radio tracking and animal populations (J. J. Millspaugh and J. M. Marzluff, Editors). Academic Press, New York, USA.

ESRI. 2000. ArcView GIS. Version 3.2a. Environmental Systems Research Institute, Inc., Redlands, California, USA.

Evans Mack, D. and Y. Wang. 2000. Swainson's Thrush (*Catharus ustulatus*). The birds of North America. Number 540.

Fink, M. 2003. Post-fledging ecology of juvenile Wood Thrush in fragmented and contiguous landscapes. Dissertation. University of Missouri, Columbia, USA.

Forsman, E. D., R. G. Anthony, J. A. Reid, P. J. Loschl, S. G. Sovern, M. Taylor, B. L. Biswell, A. Ellingson, E. C. Meslow, G. S. Miller, K. A. Swindle, J. A. Thrailkill, F. F. Wagner, and D. E. Seaman. 2002. Natal and breeding dispersal of Northern Spotted Owls. Wildlife Monographs 149.

Green, D. J. and A. Cockburn. 2001. Post-fledging care, philopatry and recruitment in Brown Thornbills. Journal of Animal Ecology 70:505–514.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Journal of Animal Behavior 28:1140–1162.

Hooge, P. N. and B. Eichenlaub. 1997. The animal movement extension to arcview. Version 1.1. USGS, Alaska Science Center—Biological Science Office, Anchorage, USA.

Horne, J. S. and E. O. Garton. 2006. Liklihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70:641–648.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* Radio tracking and animal populations (J. J. Millspaugh and J. M. Marzluff, Editors). Academic Press, New York, USA.

Kershner, E. L., J. W. Walk, and R. E. Warner. 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. Auk 121:1146–1154.

Lang, J. D., L. A. Powell, D. G. Krementz, and M. J. Conroy. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. Auk 119:109–124.

Martin, T. E. and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64: 507–519.

Otis, D. L. and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039–1044.

Pasinelli, G., J. Heglebach, and H.-U. Reyer. 2001. Spacing behavior of the Middle Spotted Woodpecker in central Europe. Journal of Wildlife Management 65:432–441.

Rappole, J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62: 335–337.

Rolando, A. 1998. Factors affecting movements and home ranges in the Jay (*Garrulus glandarius*). Journal of Zoology 246:249–257.

Roth, J. E., J. P. Kelly, W. J. Sydeman, and M. A. Colwell. 2004. Sex differences in space use of breeding Common Ravens in western Marin County, California. Condor 106:529–539.

Rush, S. 2003. The effects of forest fragmentation on post-fledging survival and dispersal of a forest songbird. Thesis. York University, Toronto, Ontario, Canada.

SAS Institute Inc. 1999. SAS/STAT user's guide. Version 8. SAS Institute Inc., Cary, North Carolina, USA.

Seaman, D. E., B. Griffith, and R. A. Powell. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95–100.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739–747.

Suedkamp Wells, K. M., J. J. Millspaugh, M. R. Ryan, and M. W. Hubbard. 2008. Factors affecting home range size and movements of post-fledging grassland birds. Wilson Journal of Ornithology 120:120–130.

Vega Rivera, J. H., C. A. Haas, J. H. Rappole, and W. J. McShea. 2000. Parental care of fledgling Wood Thrushes. Wilson Bulletin 112:233–237.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100:69–78.

White, G. C. and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, USA.

White, J. D., T. Gardali, F. R. Thompson III, and J. Faaborg. 2005. Resource selection by juvenile Swainson's Thrushes during the post-fledging period. Condor 107:388–401.

Yackel Adams, A. A., S. K. Skagen, and R. D. Adams. 2001. Movements and survival of Lark Bunting fledglings. Condor 103:643–647.

The Wilson Journal of Ornithology 120(1):74–84, 2008

SPRING MIGRATORY STOPOVER OF SWAINSON'S THRUSH ALONG THE PACIFIC COAST OF SOUTHWEST COSTA RICA

SCOTT WILSON,[1,4] KEITH A. HOBSON,[2] DOUGLAS M. COLLISTER,[3] AND AMY G. WILSON[1]

ABSTRACT.—Stopover behavior and migratory pathways of neotropical migrant birds in Central and South America have received little study. We examined stopover ecology of Swainson's Thrush (*Catharus ustulatus*) on the Osa Peninsula, Costa Rica, during spring migration, 2002–2005. Capture rates per net hour were high ($\bar{x}$ = 21.8 individuals/100 net hrs) suggesting large numbers pass through lowland coastal areas in spring. Mean passage date of males was ~6 days earlier than females. Timing of passage by age class was variable; after-second year (ASY) birds preceded second-year (SY) birds in 2 years, SYs preceded ASYs in 1 year, and both had the same mean passage date in 1 year. We also observed annual variation in relative abundance of the two age groups. Only 1.7% of marked Swainson's Thrushes were recaptured on subsequent days suggesting most individuals left the immediate area soon after initial capture. Stopover lengths ranged from 1 to 9 days, although most were <4 days. Many individuals had some energy stores on arrival (fat score ≥ 1) but reserves varied between years and tended to be lower in SYs compared to ASYs. Regression of body mass against time of day indicated that individuals tended to gain mass throughout the morning (0.67% of lean body mass/hr on average). Our findings for stopover lengths, rates of mass gain, and recapture rates are within the range observed at North American stopover sites in spring. However, our capture rates were relatively higher, perhaps because the small land mass of southern Central America concentrates individuals at stopover sites in these regions. *Received 26 September 2006. Accepted 31 March 2007.*

Annual movements between breeding and wintering areas allow neotropical migrant songbirds to benefit from the seasonal flush of food in temperate breeding areas, while enhancing survival by wintering in the tropics (Greenberg 1980). However, long-distance migration is energetically expensive and reserves required to traverse these distances may exceed the amount individuals can store (Alerstam and Lindström 1990, Schaub and Jenni 2000a). Thus, migrants need to stopover *en route* where they must forage quickly in unfamiliar habitats (Moore and Aborn 2000, Petit 2000) while coping with weather (Rappole and Warner 1976, Richardson 1978), predators (Lindström 1990), and other individuals competing for the same resources (Moore and Wang 1991). Failure to meet these demands may be costly. Most annual mortality for migrant songbirds may occur during migration even though these periods only represent ~25% of the annual cycle (Sillett and Holmes 2002). An individual's inability to refuel quickly at stopover sites can also lower fitness through delayed arrival in breeding areas and a subsequent reduction in breeding success (Marra et al. 1998, Smith and Moore 2005).

Nearly all studies of spring stopover of neotropical migrants have been conducted in North America, representing the latter half of the migration for most species. Little is known about migratory behavior and stopover ecology during the early stages of spring migration in tropical areas of Central and South America. Central America has a small landmass relative to North America and, for some species that breed across the boreal forest and winter in South America, the entire breeding population may pass through a narrow geographic corridor during migration. Even minor disturbances to stopover sites in these areas could have implications for population dynamics (Newton 2006). Deforestation and habitat disturbance have been extensive throughout much of Central America and are expected to continue (Achard et al. 2002). Thus, it is important to further our understanding of migratory routes and stopover areas used by neotropical migrants throughout sites in the tropics.

[1] Center for Applied Conservation Research, 2424 Main Mall, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada.

[2] Environment Canada, 11 Innovation Boulevard, Saskatoon, SK, S7N 3H5, Canada.

[3] Calgary Bird Banding Society, 247 Parkside Crescent SE, Calgary, AB, T2J 4J3, Canada.

[4] Corresponding author;
e-mail: wilsonwa@interchange.ubc.ca

We examined migratory timing and stopover behavior of Swainson's Thrush (*Catharus ustulatus*) at a site on the Osa Peninsula, Costa Rica. The Swainson's Thrush is a neotropical migrant that breeds across the boreal forest, western mountain regions, and Pacific coast of North America. Coastal breeding populations winter in southern Mexico and northern Central America, while continental breeding populations primarily winter in western South America (Mack and Wang 2000, Ruegg and Smith 2002). Swainson's Thrush is a common migrant in Pacific coast regions of southwestern Costa Rica in spring (Stiles and Skutch 1995), and we previously showed that individuals passing through these regions likely breed in areas of the west-central boreal forest and interior western mountains of North America (Wilson et al. 2008). Our specific objectives in the present study were to examine: (1) capture rates over time, (2) differences in migratory timing between age and gender classes, and (3) stopover length, recapture rates, and rates of mass gain.

METHODS

Study Area.—The study was conducted on the northwest tip of the Osa Peninsula, Costa Rica, during spring migration 2002–2005. Our study area (08° 41′ N, 83° 38′ W) was 3 ha in size ~10 km north of Corcovado National Park. Annual mean temperatures on the Osa Peninsula are 27° C and precipitation is 550 cm with dry and wet seasons occurring in December–April and May–November, respectively (Holdridge 1967). Habitat in the region consists of tropical wet and premontane forest (Sanchez-Azofeifa et al. 2002). The immediate study area was mostly secondary forest, 15–25 years of age, with larger stands of primary forest along the eastern and southern edges. There were two small open areas (~30 by 30 m) within the 3-ha plot. This is typical of habitat structure along coastal areas outside Corcovado National Park, where settlement has led to fragmentation and patches of younger-age forests. Much of the habitat adjacent to our site was secondary forest, particularly along the coast in both directions. The habitat beyond our site towards the interior of the peninsula was a mixture of primary and secondary forest with some cleared areas for agriculture (Sanchez-Azofeifa et al. 2002). Common tree species included *Spondias monbin*, *Hyeronima alchorneoides*, *Elaeis oleifera*, *Socratera exorrhiza*, and *Ochroma pyramidale*; common understory shrubs, vines, and small trees included *Apebia tiboubou*, *Heliconia* spp., *Vosychia* spp., *Philodendron* spp., and *Piper* spp.

Capture Methods.—The site was operated from late March through April annually. We captured individuals using 12–15 mist nets (3-tier, 12-m length, 30-mm mesh) that were opened at dawn and operated for ~6 hrs. Nets were evenly spaced throughout the study area and mostly within or on the edge of secondary forest habitats. A few were just inside primary forest at the edge of the study area. We made minor adjustments to the location of some net lanes between years because of slight changes in land use. These changes did not influence our survey effort and we do not believe they influenced our results. Individuals captured were banded with a numbered USGS aluminum band and classified to age where possible as second year (SY) or after-second year (ASY) based on plumage, feather shape and wear, and wing morphology (Pyle 1997). We also recorded date and time of capture, wing chord, body mass, and fat score (Helms and Drury 1960). We measured all individuals recaptured on subsequent days but only recorded time of capture for those recaptured on the same day. Plumage examination indicated that Swainson's Thrushes captured were from continental populations (olive-backed group) that breed across the boreal forest and interior western mountains (Mack and Wang 2000, Ruegg and Smith 2002). The Swainson's Thrush is sexually monomorpic and individuals were genetically assigned to gender following Griffiths et al. (1998) and Wilson et al. (2008). The Swainson's Thrush is a rare winter resident in the area (Stiles and Skutch 1995) and a separate study failed to capture any individuals during three 8-day periods from early December to early March 2005–2006 (D. M. Collister, unpubl. data). Thus, nearly all individuals captured were likely passage migrants.

Statistical Analyses.—Swainson's Thrushes primarily migrated through the site between late March and late April (Wilson et al. 2008). We used only 2004 and 2005 data for some analyses because data from 2002 and 2003

TABLE 1. Timing of study, effort, and capture data for Swainson's Thrushes on the Osa Peninsula, Costa Rica.

Year	Dates	Net hrs	Individuals captured	Individuals recaptured (subsequent days)
2002	17 Mar–12 Apr[a]	2,041	439	
2003	15 Apr–10 May	2,123	404	10 (2.5%)
2004	28 Mar–29 Apr	2,468	546	9 (1.6%)
2005	30 Mar–29 Apr	2,213	540	7 (1.3%)

[a] We did not band all Swainson's Thrushes in 2002 and did not estimate recapture rates for that year. A small number of the 439 captures in 2002 were likely recaptures.

were outside the late March–late April period. We used general linear models (GLM) to compare timing of migration by age and gender, and we present means with standard error for most measures. Energetic condition was compared using fat scores (Helms and Drury 1960) and residuals from a regression of mass against wing length. We used mass-wing residuals rather than deviation from the average mass because an individual's size will affect mass, and wing length is a useful way to standardize for size (Schulte-Hostedde et al. 2005). Examination of mass-wing length residuals indicated a linear relationship and no tendency for body size to influence energetic condition (Schulte-Hostedde et al. 2005). We also report fat scores for comparison with other studies but did not conduct analyses using these scores because they are a subjective measure.

We estimated stopover length by calculating minimum stopover duration where the individual's date of first capture was subtracted from the last date recaptured (Cherry 1982). This method is conservative because it does not incorporate time the bird spent at the site before first capture or after last capture. We also used open population capture-recapture models (Schaub et al. 2001). This approach uses Cormack-Jolly-Seber models to estimate the likelihood of capture for an individual present at the site and recruitment analyses to estimate probability of arrival in the study area prior to capture. Parameter estimation using this method is limited when recapture sample sizes are small, as was the case in our study. We used the multiple day constancy method of Morris et al. (2005) which holds parameters fixed across days reducing the number of parameters that need to be estimated without pooling data.

We calculated change in mass of recaptured individuals by subtracting the mass at first capture from mass at final capture. This value was divided by the stopover duration to calculate change in mass per day. We also estimated rates of mass gain by regressing mass against time of capture for all individuals because recaptured individuals may not be a random sample of the entire population (Winker et al. 1992, Dunn 2001). We included wing length in the model to control for effects of size on mass gain. The regression coefficient for time of capture represents the average change in mass per minute. We used the mass versus time of capture regression equation to estimate the expected rate of mass gain for an individual of average wing length over the 6-hr period since sunrise. Statistical analyses were conducted using the R Statistical Language and Environment package (R Development Core Team 2006).

RESULTS

Capture Rates and Migration Timing.—We captured 1,931 Swainson's Thrushes over the 4-year study. These numbers equated to 19.1, 22.1, and 24.4 Swainson's Thrushes/100 net hrs for each year, 2003–2005, respectively (Table 1). We did not band all individuals in 2002 and could not estimate recaptures. However, based on recapture rates from the other 3 years, we likely captured ~21 individuals/100 net hrs in 2002. The lower numbers in 2002 and 2003 are likely because banding did not encompass the full migratory period of Swainson's Thrushes. Data from 2002 and 2003 indicated most individuals passed through the site between late March and late April. In 2002, banding extended from 17 March to 12 April, but only 7 and 17% of individuals were caught prior to 28 March and

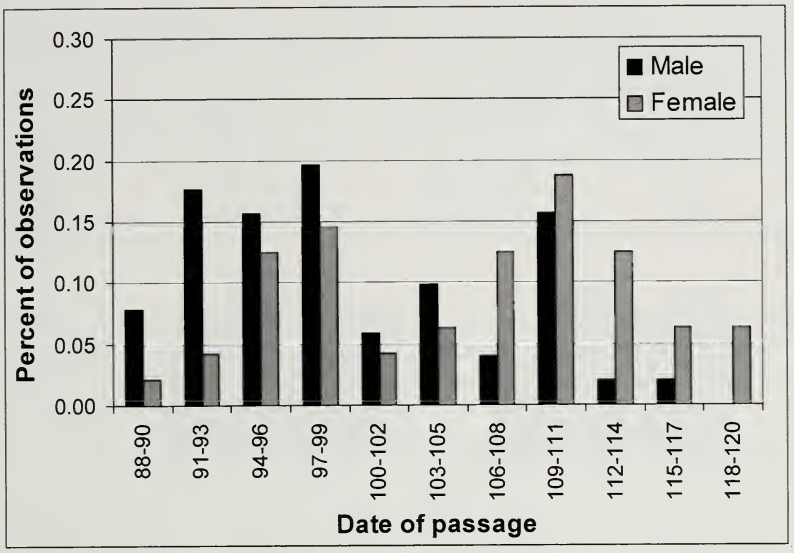


FIG. 1. Timing of spring migration of male and female Swainson's Thrushes through the Osa Peninsula, Costa Rica, in 2004 (males = 51, females = 48). Date of passage refers to Julian day with 1 Apr = 92.

30 March (start dates for 2004 and 2005), respectively. In 2003, banding was conducted from 15 April to 10 May but only 4% of individuals were caught after 29 April (end date for 2004 and 2005). We may have missed some birds, especially early in migration but our data for 2004 (28 Mar–29 Apr) and 2005 (30 Mar–29 Apr) likely represent ~80–90% of the individuals passing through the site (Fig. 1). Recapture rates during 2003–2005 were low with 10 (2.5%), 9 (1.65%), and 7 (1.3%) individuals caught on subsequent days in each year, respectively. There were no year to year recaptures.

The mean passage date of males in 2004 was ~6 days earlier than for females (males: 98 ± 1.0 (mean Julian day ± SE), n = 51; females: 104 ± 1.2, n = 48). We also examined passage date through the site with all known-age birds in 2004 and 2005. In 2004, 46% of birds captured were SY, 27% were ASY, and 27% were of unknown age. The mean passage date of ASYs (103 ± 0.6, n = 149) was ~3 days earlier than SYs (106 ± 0.5, n = 249) in 2004. Passage dates were earliest for ASY males, intermediate for SY males and ASY females, and latest for SY females for birds of known age and gender (Fig. 1). More individuals captured in 2005 were SY (84%) versus ASY (11%) but there was little difference in timing of passage between the two groups (ASY: 103 ± 0.9, n = 59; SY: 103 ± 0.4, n = 459). We only attempted to classify age of 167 of 439 individuals captured in 2002. Of these, 49% were SYs, 31% were ASYs, and 20% could not be classified to age. SY's within the shortened 2002 period passed through on average 1 day earlier than ASYs (SY: 92 ± 0.6, n = 82; ASY: 93 ± 0.9, n = 51). Of 404 individuals in 2003, 73% were SYs, 13% were ASYs, and 14% could not be classified to age. ASY's preceded SYs by 2 days on average in 2003 (SY: 111 ± 0.3, n = 295; ASY: 109 ± 0.6, n = 54). Estimates should only be compared within years because the data do not cover the same periods each year.

Stopover Length and Mass Gain.—Mean minimum stopover lengths ranged from 1 to 9 days with a mean of 3.2 days (n = 9) in 2004 and 2.3 days (n = 7) in 2005. The distribution tended to be skewed as 14 of 16 individuals had stopover lengths of 1–4 days while two stayed for 6 and 9 days. The median minimum stopover length was 2 days in both years. Stopover lengths estimated by the multiple day constancy (MDC) method were 4.0 ± 3.9 days (mean ± SD) in 2004 and 1.2 ± 0.7 days in 2005. The minimum stopover duration and MDC capture-recapture methods produced similar results with the capture-recapture method estimating slightly longer

TABLE 2. Regression coefficients for equation of mass against wing chord and time of capture for Swainson's Thrushes on the Osa Peninsula, Costa Rica. Standard errors are in parentheses. Time represents average change in mass (grams) per minute.

Class	*n*	Intercept	Wing chord	Time
All birds	1,042	1.096 (2.10)	0.278 (0.022)	0.003 (0.0007)
ASY	201	0.924 (4.72)	0.283 (0.048)	0.0018 (0.0017)
SY	675	−1.153 (2.73)	0.302 (0.029)	0.0036 (0.0009)

stopovers in 2004 and shorter stopovers in 2005. We did not compare stopover length by age and gender because of the low number of recaptures.

Regression equations for body mass against wing chord and time of capture indicated a significant influence of both wing and time since sunrise on body mass ($R^2 = 0.15$, $F_{2,1039} = 92.65$, $t_{wing} = 12.89$, $P_{wing} < 0.001$, $t_{time} = 4.79$, $P_{time} < 0.001$, Table 2). We predicted from the regression equation that an average-sized individual (mean wing = 95.7 mm) would add about 1.08 grams over the 6-hr period from sunrise equating to 0.18 g/hr. This estimate would be ~0.67% of lean body mass/hr using the average mass for individuals with a fat score of 0. We examined age effects on rates of body mass gain by regressing mass against time of capture for SYs and ASYs separately. The equation for SYs revealed a significant effect of wing length and time since sunrise on mass ($R^2 = 0.16$, $\beta_{wing} = 0.30$ (SE = 0.03), $P_{wing} < 0.001$, $\beta_{time} = 0.004$ (SE = 0.001), $P_{time} < 0.001$). We predict an average-sized SY individual with a mean wing length of 95.3 mm would add 1.3 g over the 6-hr morning period. Wing chord for ASYs had a significant effect but time since sunrise did not although the coefficient was positive ($R^2 = 0.15$, $\beta_{wing} = 0.28$ (SE = 0.05), $P_{wing} < 0.001$, $\beta_{time} = 0.002$ (SE = 0.002), $P_{time} = 0.284$).

Analysis of fat reserves at time of banding revealed that most individuals had some fat (72.5% of individuals had a fat score ≥1, Fig. 2). There was a tendency for ASYs to have higher fat scores than SYs and higher fat scores in 2004 than 2005 for both groups. Measures of energetic condition from residuals of a mass-wing regression did not reveal distinct differences by age or gender and there was variability within classes. Residual estimates for each group were [mean ± SE (*n*)] ASY male: 0.43 ± 0.51 g (14), SY male: 0.44 ± 0.44 g (21), ASY female: −0.06 ± 0.49 g (14), SY: female −0.10 ± 0.32 g (25). Recaptured and non-recaptured individuals had similar fat scores (mean ± SE) (recapture = 1.4 ± 0.35, non-recapture = 1.5 ± 0.05). Analyses of mass change from recaptured birds revealed variability among individuals. Seven of 15 individuals in 2004 and 2005 lost mass during the stopover (average loss = 0.6 g/day) while 8 gained mass (average gain = 0.3 g/day). The average mass change based on these individuals was lower than predicted by regressing mass against time of capture using all birds.

DISCUSSION

Captures.—Swainson's Thrushes were common spring migrants at a stopover site along the Osa Peninsula, Costa Rica. This species is a rare winter resident in the region and all individuals captured were likely passage migrants. Individuals from South American wintering areas likely reached the study site by following the Panama isthmus or via an ocean crossing from Colombia making landfall between the Azuero Peninsula of Panama and the Osa Peninsula of Costa Rica (Wilson et al. 2008). Swainson's Thrushes are also common spring migrants along the Caribbean coast of Central America (Galindo et al. 1963, Ridgely and Gwynne 1989, Ralph et al. 2005). Most continental birds enter North America along the Gulf coast (Rappole and Warner 1976; Wang and Moore 1993, 1997) before moving to breeding locations across the boreal forest and mountainous areas from Alaska to eastern Canada and the northeastern United States (Mack and Wang 2000, Ruegg and Smith 2002).

Swainson's Thrush capture rates averaged 20–25 individuals/100 net hrs and are among the highest reported for this species in spring.

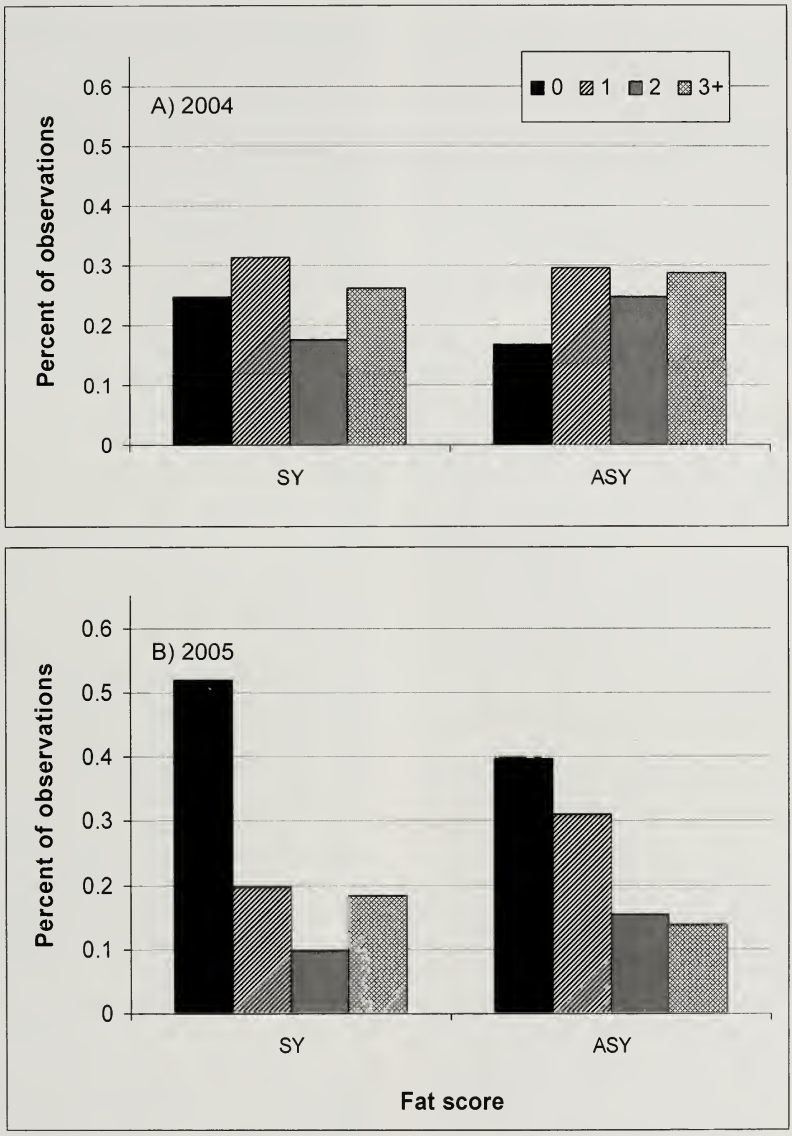


FIG. 2. Fat scores for second year (SY) and after-second year (ASY) Swainson's Thrushes on the Osa Peninsula, Costa Rica, in (A) 2004 (SY = 249, ASY = 149) and (B) 2005 (SY = 450, ASY = 58).

Spring capture rates along the northern Gulf coast of Mexico for four thrush species combined were ~8–10 individuals/100 net hrs; Swainson's Thrushes accounted for about 36% of those captures (Wang and Moore 1997). Elsewhere, spring capture rates of Swainson's Thrushes (individuals/100 net hrs) were 0.49 in Minnesota (Winker et al. 1989), 1.5 in southern Alberta (Collister et al. 2005), and 2.35 in South Dakota (Swanson et al. 2003). At Almirante on the Caribbean coast of Panama, 365 Swainson's Thrushes were captured during netting in April 1963 (net hrs not available, Galindo et al. 1963), slightly lower than numbers caught in April at our site. Caution is required when inferring abundance from capture rates of mist-net studies because of differences in methodology, effort, dates of study, and habitat (Remsen and Good 1996). Mist-netting studies may also be biased against larger species and those that primarily inhabit the canopy and subcanopy layers

(Blake and Loiselle 2001). Swainson's Thrushes primarily forage in lower forest levels (Mack and Wang 2000) and were usually observed in the understory at our site. Thus, mist-net captures likely provide an accurate index of abundance for this species. The high number of captures in our study relative to North American sites may have been due to the small landmass of southern Central America, which likely concentrates individuals during migration.

Migration Timing.—Males passed through the site ~6 days earlier than females in 2004 with mean passage dates of 6 April and 12 April, respectively. Few studies have examined gender differences in migratory timing of *Catharus* thrushes because they are sexually monomorphic and require genetic techniques to accurately ascertain gender. Wing lengths of migrating thrushes along the Gulf coast in spring declined over time, suggesting earlier passage of larger males (Wang and Moore 1997). A similar pattern was noted among Swainson's Thrushes at a spring stopover site in Minnesota (Winker et al. 1989). Gender-specific spring migration patterns are frequently reported in sexually dimorphic species (Francis and Cooke 1986, Wang et al. 1998, Swanson et al. 1999). Mean passage date of male Northern Wheatears (*Oenanthe oenanthe leucorhoa*) in Scandinavia was 5 days earlier than females (Dierschke et al. 2005) while on Appledore Island, Maine, male American Redstarts (*Setophaga ruticilla*) and Common Yellowthroats (*Geothlypis trichas*) preceded females by 2 and 5 days, respectively (Morris and Glasgow 2001, Morris et al. 2003).

Earlier spring passage of males is likely related to male-male competition in breeding areas and the need for males to establish territories prior to arrival of females (Lack 1954). Earlier passage of males through stopover sites could be due to: (1) earlier departure from wintering areas (Marra et al. 1998), (2) faster migration rates (Swanson et al. 1999), or (3) more northerly wintering areas and a shorter distance to stopover sites (Chandler and Mulvihill 1990). Although our site was relatively close to wintering areas, differences between males and females were similar to patterns from other species at North American stopover sites. This might suggest that earlier passage of males was due to earlier departure and/or more northern wintering areas, although it is still possible that males travel more quickly than females in spring.

We found mixed results for age-specific timing of migration. Using all known-age individuals, ASYs preceded SYs by about 3 days in 2004 but the two groups had similar mean passage dates in 2005. Within the shortened study periods in the first 2 years, SYs preceded ASYs by 1 day in 2002 and ASYs preceded SYs by 2 days in 2003. However, these data were based on all known-age birds and, given gender-specific differences in passage date, it is difficult to interpret timing by age group when males and females are pooled. Furthermore, there tended to be more unknown age individuals at the start of the season, which may not have been equally representative of both age groups. Although the sample size was smaller, our data for individuals of known age and gender in 2004 may be most informative and indicated that ASY males passed through earliest, SY males and ASY females were intermediate, and SY females were the latest to arrive. This is consistent with earlier migration by males and a tendency for older birds to precede first-year birds (Francis and Cooke 1986, Stewart et al. 2002). We are uncertain why there was annual variation in age ratios. There was a relatively higher proportion of ASYs in 2002 and 2004 than in 2003 and 2005. Annual variation in the abundance of age groups at stopover sites may be due to greater productivity the previous spring, age-specific differences in survival, or variability in the routes or stopovers sites used by different age groups (Ralph 1981, Wang et al. 1998, Dean et al. 2004). Changes in study design or survey effort may also influence age ratios at stopover sites (Kelly and Finch 2000). Our data from 2002 and 2004 included a higher number of individuals from the early migratory period which, if there was a tendency for older birds to move earlier, may explain the higher proportion of ASYs captured in those years. Further research on variation in the abundance and timing of passage by age class at other tropical stopover sites would be useful.

Stopover Ecology.—Only 26 of 1,490 individuals (1.7%) captured in 2003 to 2005 were recaptured on subsequent days suggesting the majority of individuals moved from

the study area soon after capture. Spring recapture rates were similar to those from the St. Croix River Valley, Minnesota (1.2%, Winker et al. 1989) but were lower than rates observed elsewhere. Recapture rates were 9 and 7% from two separate studies along the northern Gulf coast (Kuenzi et al. 1991, Wang and Moore 1997), 5.7% along coastal regions of south Texas (Rappole and Warner 1976), and 5.2% along the Caribbean coast of Panama (Galindo et al. 1963).

One reason for the low recapture rate at our study site may have been that it was small (3 ha) with extensive areas of similar nearby habitat. Thus, individuals may continue to move through these habitats without returning to the study site. Recapture rates may be higher at sites that are spread over a wider region increasing the likelihood of capturing individuals that wander but remain within the general area. Galindo et al. (1963), on the Caribbean coast of Panama, surveyed four plots over a 25.9 km^2 area and recorded higher recapture rates. Cochran and Wikelski (2005), using radio-telemetry, found that Swainson's Thrushes at stopover sites in Illinois established small foraging areas of ~100 m in diameter and remained in that area until the next flight. However, the large number of individuals at our site may have influenced how many remained in the area (Moore and Wang 1991, Wang et al. 1998). Differences in food abundance between locations may also lead to variation in stopover behavior and recapture rates (e.g., Petit 2000).

Individuals may also be less likely to remain at stopover sites if they have sufficient reserves to continue on migration. Stopover length is often negatively related to energetic condition (Moore and Kerlinger 1987, Cochran and Wikelski 2005). Experimental studies have found that, following a trans-Gulf crossing, individuals with greater energetic reserves have higher migratory restlessness than those in poor condition (Wang and Moore 1993, but see Smith and Norment 2005). Multi-day stopovers may be necessary if all fat reserves are depleted, as is often the case along the gulf coast (e.g., Kuenzi et al. 1991). Many individuals in our study had fat scores ≥ 1 and gained mass through the morning, which combined may provide sufficient reserves to continue on that night. Migrants at stopover sites in Costa Rica would also not cross a major geographic barrier until they reached the Gulf of Mexico and it may not be necessary to build reserves beyond what is required for a few hours of flight (e.g., Schaub and Jenni 2000b, Rubolini et al. 2002). Individuals that did stopover typically remained for ~1 to 4 days, similar to lengths observed for this species in temperate areas further north (Winker et al. 1989, Wang and Moore 1997).

Rates of mass gain through the morning averaged ~0.18 g/hr, which equates to 0.67% of the lean body mass (average mass of individuals with no visible fat) (Dunn (2002). This is similar to the pooled estimates for spring migrants across Canada (0.40% of lean body mass), although rates for Swainson's Thrushes in that study were low (average = −0.06% of lean body mass/hr, Dunn 2001, 2002). Daily mass gain for Swainson's Thrushes in Minnesota (Winker et al. 1989) was ~4.08 g/day in spring, slightly higher than our data. Variation in rates of mass gain among sites could be due to differences in food availability (Dunn 2001) or whether migrants are using a site for other purposes such as to rest or rehydrate (Kuenzi et al. 1991).

Entire populations of some neotropical migrant species may pass through a narrow geographic corridor during early stages of spring migration because of the small landmass of southern Central America. Habitat disturbance in these regions could negatively impact populations of these species (Sillett and Holmes 2002, Newton 2006). We know little about migratory routes, habitat requirements, and stopover behavior of neotropical migrants in tropical regions. Our study revealed that Swainson's Thrush use lowland habitats along Costa Rica's Pacific coast in spring; high numbers relative to North American sites indicate thrushes are particularly concentrated during this period. Recapture rates, stopover lengths, and rates of mass gain were similar to those in temperate areas suggesting these behaviors may be consistent across the spring migratory period. Studies that use a combination of mist netting and counts in high and low elevation habitats of southern Central America would further our knowledge of stopover ecology of neotropical migrant songbirds within the tropics.

ACKNOWLEDGMENTS

We thank S. R. Morris for conducting analyses on stopover length using capture-recapture methods, C. E. Ritland, A. E. Miscampbell, and H. H. Yeh for help with genetic analyses, and Rex Kenner for assisting with gender classification of museum specimens. We also thank Jolanda Hess, David Argello, and Jay Tress for access to their property. Yong Wang and an anonymous reviewer provided valuable comments on an earlier draft of this manuscript. We thank members of the Calgary Bird Banding Society (A. M. Cole, Jen Lane, Steve Lane, P. E. Mitchell, Mike Mulligan, E. A. Peterson, Carl Savignac, G. J. Smiley, W. P. Taylor, B. R. Trakalo, and C. M. Watson) and Alberto and Elizabeth Quesada-Calvo for assistance in the field. Funding for this project was provided by members of the Calgary Bird Banding Society, Alberta Gaming and Liquor Commission, Canadian Wildlife Service, NSERC (doctoral grants to SW, AGW) and a Killam doctoral award to SW.

LITERATURE CITED

ACHARD, F., H. D. EVA, H. J. STIBIG, P. MAYAUX, J. GALLEGO, T. RICHARDS, AND J. P. MALINGREAU. 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297:999–1002.

ALERSTAM, T. AND Å. LINDSTRÖM. 1990. Optimal bird migration: the relative importance of time, energy and safety. Pages 331–351 *in* Bird migration: physiology and ecophysiology (E. Gwinner, Editor). Springer-Verlag, Berlin, Germany.

BLAKE, J. G. AND B. A. LOISELLE. 2001. Bird assemblages in second growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. Auk 118:304–326.

CHANDLER, C. R. AND R. S. MULVIHILL. 1990. Interpreting differential timing of capture of sex classes during spring migration. Journal of Field Ornithology 61:85–89.

CHERRY, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. Auk 99:725–732.

COCHRAN, W. W. AND M. WIKELSKI. 2005. Individual migratory tactics of New World *Catharus* thrushes: current knowledge and future tracking options from space. Pages 274–289 *in* Birds of two worlds (R. Greenberg and P. P. Marra, Editors) Johns Hopkins University Press, Baltimore, Maryland, USA.

COLLISTER, D. M., R. D. DICKSON, AND G. SMILEY. 2005. 2004 Calgary Bird Banding Society Annual Technical Report. Calgary, Alberta, Canada.

DEAN, K. L., H. A. CARLISLE, AND D. L. SWANSON. 2004. Age structure of neotropical migrants during fall migration in South Dakota: is the northern Great Plains region an inland "coast"? Wilson Bulletin 116:295–303.

DIERSCHKE, V., B. MENDEL, AND H. SCHMALJOHANN. 2005. Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? Behavioral Ecology and Sociobiology 57:470–480

DUNN, E. H. 2001. Mass change during migration stopover: a comparison of species groups and sites. Journal of Field Ornithology 72:419–432.

DUNN, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson Bulletin 114:368–379.

FRANCIS, C. M. AND F. COOKE. 1986. Differential timing of spring migration in wood warblers (Parulinae). Auk 103:548–556.

GALINDO, P., E. MENDEZ, AND A. J. ADAMES. 1963. Banding of migrant thrushes in Almirante, Panama. Bird Banding 34:202–209.

GREENBERG, R. 1980. Demographic aspects of long-distance migration. Pages 493–516 *in* Migrants in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, D.C., USA.

GRIFFITHS, R., M. C. DOUBLE, K. ORR, AND R. J. G. DAWSON. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

HELMS, C. W. AND W. H. DRURY. 1960. Winter and migratory weight and fat: field studies on some North American buntings. Bird-Banding 31:1–40.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

KELLY, J. F. AND D. M. FINCH. 2000. Effects of sampling design on age ratios of migrants captured at stopover sites. Condor 102:699–702.

KUENZI, A. J., F. R. MOORE, AND T. R. SIMONS. 1991. Stopover of neotropical landbird migrants on East Ship Island following Trans-Gulf migration. Condor 93:869–883.

LACK, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, United Kingdom.

LINDSTRÖM, Å. 1990. The role of predation risk in stopover habitat selection in migrating Bramblings *Fringilla montifringilla*. Behavioral Ecology 1: 102–106.

MACK, D. E. AND Y. WANG. 2000. Swainson's Thrush (*Catharus ustulatus*). The birds of North America. Number 540.

MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282: 1884–1886.

MOORE, F. R. AND D. A. ABORN. 2000. Mechanism of *en route* habitat selection: how do migrants make habitat decisions during stopover? Studies in Avian Biology 20:34–42.

MOORE, F. R. AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47–54.

MOORE, F. R. AND Y. WANG. 1991. Evidence of food-based competition during migratory stopover. Behavioral Ecology and Sociobiology 28:85–90.

Morris, S. R. and J. L. Glasgow. 2001. Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. Wilson Bulletin 113: 202–210.

Morris, S. R., C. R. Pusateri, and K. A. Battaglia. 2003. Spring migration and stopover ecology of Common Yellowthroats on Appledore Island, Maine. Wilson Bulletin 115:64–72.

Morris, S. R., D. A. Liebner, A. M. Larracuente, E. M. Escamilla, and H. D. Sheets. 2005. Multiple day constancy as an alternative to pooling for estimating mark-recapture stopover length in Nearctic-neotropical migrant landbirds. Auk 122:319–328.

Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147:146–166.

Petit, D. R. 2000. Habitat use by landbirds along Nearctic-neotropical migration routes: implications for conservation of stopover habitats. Studies in Avian Biology 20:15–33.

Pyle, P. 1997. Identification guide to North American birds. Part I. Slate Creek Press, Bolinas, California, USA.

R Development Core Team. 2006. R: a language and environment for statistical computing, reference index version 2.3.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (accessed 24 February 2007).

Ralph, C. J. 1981. Age ratios and their possible use in determining autumn routes of migrant passerines. Wilson Bulletin 93:164–188.

Ralph, C. J., M. J. Widdowson, R. I. Frey, P. A. Herrera, and B. P. O'Donnell. 2005. An overview of a landbird monitoring program at Tortuguero, on the Caribbean coast of Costa Rica. USDA, Forest Service, General Technical Report PSW-GTR-191. Albany, California, USA.

Rappole, J. H. and D. W. Warner. 1976. Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26:193–212.

Remsen, J. V. and D. A. Good. 1996. Misuse of data from mistnet captures to assess relative abundance in bird populations. Auk 113:381–398.

Richardson, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

Ridgely, R. S. and J. A. Gwynne. 1989. A guide to the birds of Panama. Princeton University Press, Princeton, New Jersey, USA.

Rubolini, D., A. G. Pastor, A. Pilastro, and F. Spina. 2002. Ecological barriers shaping fuel stores in Barn Swallows *Hirundo rustica* following the central and western Mediterranean flyways. Journal of Avian Biology 33:15–22.

Ruegg, K. C. and T. B. Smith. 2002. Not as the crow flies: a historical explanation for circuitous migration in Swainson's Thrush (*Catharus ustulatus*). Proceedings of the Royal Society of London Series B 269:1375–1381.

Sanchez-Azofeifa, G. A., B. Rivard, J. Calvo, and I. Moorthy. 2002. Dynamics of tropical deforestation around national parks: remote sensing of forest change on the Osa Peninsula of Costa Rica. Mountain Research and Development 22:352–358.

Schaub, M. and L. Jenni. 2000a. Body mass of six long-distance migrant passerine species along the autumn migration route. Journal für Ornithologie 141:441–460.

Schaub, M. and L. Jenni. 2000b. Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317.

Schaub, M., R. Pradel, L. Jenni, and J. D. Lebreton. 2001. Migrating birds stopover longer than usually thought: an improved capture-recapture analysis. Ecology 82:852–859.

Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163.

Sillett, T. S. and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71: 296–308.

Smith, R. J. and F. R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

Smith, S. B. and C. J. Norment. 2005. Nocturnal activity and energetic condition of spring landbird migrants at Braddock Bay, Lake Ontario. Journal of Field Ornithology 76:303–310.

Stewart, R. L. M., C. M. Francis, and C. Massey. 2002. Age related timing of spring migration within sexes in passerines. Wilson Bulletin 114: 264–271.

Stiles, F. G. and A. F. Skutch. 1995. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

Swanson, D. L., H. A. Carlisle, and E. T. Liknes. 2003. Abundance and richness of neotropical migrants during stopover at farmstead woodlots and associated habitats in southeastern South Dakota. American Midland Naturalist 149:176–191.

Swanson, D. L., E. T. Liknes, and K. L. Dean. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant Ruby-crowned Kinglets. Wilson Bulletin 111:61–69.

Wang, Y. and F. R. Moore. 1993. Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. Condor 95:934–943.

Wang, Y. and F. R. Moore. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114: 263–278.

Wang, Y., D. M. Finch, F. R. Moore, and J. F. Kelly. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. Auk 115:829–842.

Wilson, S., K. A. Hobson, D. M. Collister, and A. G. Wilson. 2008. Breeding destinations and

spring migration patterns of Swainson's Thrush at a Costa Rican stopover site. Auk 125: In Press.

WINKER, K., D. W. WARNER, AND A. R. WIESBROD. 1989. The Northern Waterthrush and Swainson's Thrush as transients at a temperate inland stopover site. Pages 384–404 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Editors). Smithsonian Institution Press, Washington D.C., USA.

WINKER, K., D. W. WARNER, AND A. R. WIESBROD. 1992. Daily mass gains among woodland migrants at an inland stopover site. Auk 109:853–862.

The Wilson Journal of Ornithology 120(1):85–91, 2008

DEMOGRAPHY OF EASTERN YELLOW WAGTAILS AT CAPE ROMANZOF, ALASKA

HEATHER M. RENNER[1,3,4] AND BRIAN J. McCAFFERY[2]

ABSTRACT.—We quantified demographic parameters of Eastern Yellow Wagtails (*Motacilla tschutschensis*) breeding at Cape Romanzof, Yukon Delta National Wildlife Refuge, Alaska. We monitored 79 nests in an 837-ha area during 1997–1999 and banded 160 individuals. Mayfield nest success differed among years and ranged from 0.14 to 0.63/year. Most nest failures were attributed to predation. Annual fecundity (mean number of fledglings/female) ranged from 0.7 to 3.7. At least 8.8% of nests had polygynous males; females paired with polygynous males had the same fecundity as monogamous females. Forty-two to 100% of the breeding males returned the following year, usually to the same territory while no adult females returned. Four nestlings banded in the study area returned to nest the following year. The best model for annual survival accounted for differences between both age groups and years. The demography of Eastern Yellow Wagtails at Cape Romanzof varied and was characterized by relatively high adult male survival and site fidelity, female-biased dispersal, and weak natal philopatry. The absence of returning females is significant and possible differences in migration stopovers and wintering locations should be investigated. Moderate levels of male immigration may be necessary in periodic pulses to maintain a local population, but female immigration would need to be massive and sustained. *Received 8 September 2006. Accepted 17 June 2007.*

Four major demographic factors affect life history patterns in bird populations: age-specific fecundity, recruitment, survival from fledging to breeding, and adult survival (Nur and Sydeman 1999). These factors can be difficult to evaluate because individuals are rarely seen after hatching or fledging. Some species of migratory birds demonstrate fidelity to breeding sites over a period of years allowing mark-recapture techniques to be used to estimate demographic parameters.

Demographic parameters have been estimated for few long-distance migrant passerines in North America. Specifically, survival estimates based on recaptures of banded birds are rare in the published literature, although recent publication of Monitoring Avian Productivity and Survivorship (MAPS) data online (Michel et al. 2006) provided estimates for many species. Other than MAPS data for Arctic Warbler (*Phylloscopus borealis*), demographic parameters have not been reported for any of the other five Paleotropic passerine species nesting in western Alaska: Bluethroat (*Luscinia svecica*), Northern Wheatear (*Oenanthe oenanthe*), White Wagtail (*Motacilla alba*), Eastern Yellow Wagtail (*M. tschutschensis*), and Red-throated Pipit (*Anthus cervinus*). Our objective in this 3-year study was to obtain the first demographic information for one of these species. Specifically, we quantified the following demographic parameters of Eastern Yellow Wagtails breeding at Cape Romanzof, Alaska: reproductive success, annual adult and first-year survival, site fidelity and natal philopatry, and earliest age at first reproduction.

METHODS

Study Area.—We studied Eastern Yellow Wagtails at Cape Romanzof Long Range Radar Site, Alaska (61° 49′ N, 166° 5′ W) during May to August 1997–1999. Cape Romanzof projects into the Bering Sea at the western end of the Askinuk Mountains between Scammon and Kokechik bays. The Askinuk Mountains rise from the delta lowlands at sea level to 714 m and extend inland about 50 km. Dwarf shrub meadows and block-fields dominate the study area which includes two drainages, Nilumat and South creeks.

Nest Searching, Capturing Birds, and Banding Protocols.—We searched for nests soon after Eastern Yellow Wagtails arrived in breeding areas in late May by watching adults fly to the nest, (a) with nesting materials or

[1] Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA.

[2] Yukon Delta National Wildlife Refuge, U.S. Fish and Wildlife Service, P. O. Box 346, Bethel, AK 99559, USA.

[3] Current address: Alaska Maritime National Wildlife Refuge, U.S. Fish and Wildlife Service, 95 Sterling Highway, Suite 1, Homer, AK 99603, USA.

[4] Corresponding author;
e-mail: heather_renner@fws.gov

with food, or (b) after mobbing potential predators (including human observers). Nests were marked with flags >5 m distant to minimize the likelihood of attracting predators to the nest. We used mist nets to capture adults at nest sites in 1997–1999 and we marked individuals with standard USGS aluminum leg bands as well as unique combinations of three color-bands. We captured adults only after eggs had hatched to minimize the risk of nest abandonment.

We marked chicks with aluminum leg bands prior to fledging in 1997 and 1998. We recorded natural fledging dates in 1997 and banded young only after at least one individual in the nest had departed to avoid premature fledging due to our activities. We attempted to mark every nestling that fledged on the study area in 1998 by banding them in the nest as soon as they were sufficiently large to retain a band, generally 10 days after hatching. We did not color-band nestlings because portions of their tarsi were too large to accommodate more than one band. We also captured Eastern Yellow Wagtails distant from nest sites in mist nets after young had fledged in both 1997 and 1998 to document post-fledging movements of previously banded hatching-year birds, and to mark adults and fledglings not previously banded. We operated an array of 6–13 mist nets around our camp and at the beach near the mouth of Nilumat Creek daily during late July and August from 0600 to 1300 hrs (weather permitting).

Reproductive Success.—We checked nests at least twice each week during the egg-laying and incubation periods, and every second day after hatching. We recorded the contents of the nest as well as presence/absence of adults and of mobbing behavior. We defined fledging as successful nest departure, although the chicks could not necessarily fly at this age. Nests from which at least one young fledged were considered successful. We confirmed fledging by observing fledglings or adults carrying food in the immediate nest area. We attributed nest failure to abandonment if eggs or dead chicks remained in the nest bowl and, otherwise to predation.

We estimated daily survival rate (s), and Mayfield nest success (P_2) (Mayfield 1960, 1975; Klett et al. 1986) for all nests with ≥2 visits while the nest was active. The estimated number of exposure days for a successful nest varied slightly each year (Renner and McCaffery 2006). We calculated confidence intervals for daily survival using Johnson's (1979) formula to compare Mayfield nest success and daily survival between years. Hatching (chicks/eggs) and fledging success were calculated for each year and for all 3 years combined. All nests were not included in this analysis; for example, if we found a nest after hatching, we were unable to ascertain the original clutch size.

Return Rate and Dispersal.—We defined a returning bird as a banded bird that nested in the study area in 1 year and was observed in the study area during the following year. A recaptured bird was one that was previously captured in the study area during the same year. A local bird was a young-of-the-year that was definitely raised in the study area. A hatching-year (HY) bird was a young-of-the-year that may have been raised in the study area. This latter definition refers to unbanded birds captured in the post-fledging mist net array that were sufficiently developed to be capable of sustained flight. Breeding dispersal distance is the distance between nests of an individual in consecutive years (Haas 1990). Distances between nests in consecutive years were measured with a 50-m tape or, when the distance exceeded 500 m, on a 1:25,000 topographic map.

We used a 20–60× spotting scope to identify banding status whenever adults were observed. In some cases, returning adults had not been color banded and were captured to identify the individual from its metal band. We calculated return rates by dividing the number of banded birds that returned to breed on the study site in the current year by the total number of banded birds breeding on the study site in the previous year (Haas 1998). We considered all marked adults that were reobserved or recaptured, regardless of whether or not their nests were found, to have returned. We evaluated the effect of nest success in year n on the probability of returning in year $n + 1$ using 2×2 contingency tables and Fisher's exact test.

Local Annual Survival Estimates.—Annual apparent survival (actual survival minus dispersal) was estimated using program MARK (White and Burnham 1999) following Lebre-

TABLE 1. Nest success of Eastern Yellow Wagtails at Cape Romanzof, Alaska, 1997–99. The Mayfield exponent is the estimated number of exposure days for a successful nest (from Renner and McCaffery 2006).

Year	# nests monitored (# successful)	Mayfield success	Mayfield exponent	Daily survival rate	95% CI for s
1997	28 (20)	0.632	28.15	0.984	0.973–0.995
1998	34 (14)	0.332	27.08	0.960	0.942–0.978
1999	17 (2)	0.136	28.00	0.931	0.897–0.965

ton et al. (1992) and Nichols et al. (1993). No marked birds were seen that had not been marked or seen in the previous year and the probability of reobservation could not be distinguished from 1. The probability of reobservation was assumed to be high and "known fate" survival estimates were calculated (Pollock et al. 1989a, b). Known fate parameter estimates assume that if birds were not observed, they did not survive (return to the population). Known fate models typically estimate actual survival but, in this case, they estimate only apparent survival. Model notation followed Lebreton et al. (1992). The factorial structure of the model is represented by subscripting the primary survival parameter (S) using "t" for annual differences and "g" for group (age, adult or juvenile, at banding) differences. Constancy over time is indicated with a dot (.). Relationships among factors were indicated using standard linear model notation.

We first defined potential models for each year separately and all years considered together (Burnham and Anderson 1998). The candidate model set included a fully parameterized global model and a series of reduced parameter models involving the survival rate. Model selection was based on comparison of the Akaike Information Criterion (AIC_c). The model with the lowest AIC_c was accepted as being most parsimonious for the data. Comparisons among models in the candidate model set were based on indices of relative model plausibility using Akaike weights (Burnham and Anderson 1998). The ratio of Akaike weights between any two models indicates the relative extent to which a particular model is better supported by the data than the other model. We report parameter estimates and associated standard errors derived by averaging over all models in the candidate model set weighted by Akaike model weights to account for uncertainty in model selection (Buckland et al. 1997, Burnham and Anderson 1998).

RESULTS

Nest Searching and Banding.—We monitored 79 nests during 1997–1999 in the Nilumat and South Creek drainages. We banded 9 adults, 9 local nestlings, and 43 HYs in 1997. All adults banded were successful breeders. In 1998, we banded 35 adults, 61 local nestlings, and 3 HYs. We captured at least one adult at all 14 successful nests including the males at 13 (93%) and the females at 11 (79%). We captured males at only 6 of 20 (30%) unsuccessful nests and females at 7 of 20 (35%) unsuccessful nests. We captured 49 HY birds during post-fledging mist-netting operations at the mouth of Nilumat Creek of which three were recaptures from elsewhere on our study site.

Reproductive Success.—Nest success was highest in 1997 and lowest in 1999 (Table 1). These 2 years differed more than four fold (i.e., non-overlapping 95% confidence intervals for s and P_2); 1998 did not differ significantly from either year. Mean number of fledglings per female ranged from 0.67 to 3.71 across the 3 years (n = 72 nests with known fates; Table 2) and all years differed (ANOVA, df = 2, $P < 0.05$; Tukey's pairwise comparisons, $P < 0.05$). Mean fecundity was higher for polygynous than for monogamous males ($P < 0.05$). Breeding success of females did not differ between those mated to monogamous and polygynous males. Polygynous males averaged 4.67 young fledged/male (n = 7 [nests of 3 males in 3 years], SE = 2.91), whereas 7 females averaged 2 fledglings per female (SE = 0.78).

Causes of Nest Failure.—We did not observe nest predation, but assumed it was the major cause of nest failure at Cape Romanzof based on frequent observations of Long-tailed

TABLE 2. Measures of fecundity for 72 Eastern Yellow Wagtail nests at Cape Romanzof, Alaska, 1997–99.

Parameter	Measure
Number eggs laid	396 (mean clutch size = 5.5)
Number eggs hatched (%)	301 (76)
Number eggs fledged (%)	148 (37)
Proportion hatched eggs that fledged young	49%
Mean ± SE fledglings/female	2.1 ± 0.30 (range 0–6, n = 72)
Mean ± SE fledglings/successful female	4.4 ± 0.20 (range 2–6, n = 38)
Mean ± SE fledglings/monogamous male	2.2 ± 0.32 (range 0–6, n = 65)
Mean ± SE fledglings/polygynous male	4.7 ± 2.91 (range 0–10, n = 3)

Jaegers (*Stercorarius longicaudus*) hunting near Eastern Yellow Wagtail nest sites, as well as red fox (*Vulpes vulpes*) and weasels (*Mustela* spp.) being mobbed by wagtails and other ground-nesting birds. We observed no obviously weather-related mortality. Predation of young probably accounted for all nest failures in 1997 (8) and 1999 (15), and most in 1998 (17). Three nests were abandoned by the parents in 1998; one after part of the clutch was lost to predators during incubation and two during early brood-rearing. Neither of the abandonments during brood-rearing was related to banding, because we had not attempted to capture birds at those nests.

Return Rate.—Overall return rates were 52% (males), 0% (females), and 26% (genders combined). None of 23 banded adult females returned to the study site in any year after banding. All four adult males banded in 1997 returned to the study area in 1998. At least 8 (42%) of the 19 adult banded males present in 1998 (including 1997 returns), returned in 1999. Four nests were lost to predators before we could learn if the males were banded; the return rate of males in 1999 may have been as high as 63%.

At least two of the four males banded in 1997 returned in 1999. One of these did not nest in 1999, but sang and displayed persistently throughout the season. Return rates for males, females, and both genders combined did not differ between those that nested successfully and unsuccessfully, respectively, in the previous year (Fisher's exact test, P = 0.26). Ten of 17 (59%) successful males and 2 of 6 (33%) unsuccessful males returned the following year; no females returned. Return rates were 30% (10/33) for successful and 15% (2/13) for unsuccessful birds when genders were combined. We were less likely to capture birds at nests that eventually failed, because some nests did not survive until our scheduled trapping day. We had a small marked sample of "unsuccessful" breeders, particularly in 1998, and the power to detect differences in return rates of successful breeders was low.

Dispersal/Site Fidelity.—Eleven of 12 returning males in 1998 and 1999 nested. Mean breeding dispersal distance for these 11 birds was 64.3 ± 32.3 m (range = 0–300 m). Two males used the same nest bowl as in the previous year. Ten of the 12 returns had nested successfully in the previous year. All returning adults nested in the same drainage as in the previous year and exhibited fidelity to their previous year's breeding territory. The two that did not eventually nest on their previous territory were often observed displaying there early in the spring and, in both cases, apparently moved because snow covered most of the territory until long after nest-building had begun in the rest of the population.

Natal Philopatry.—One of 70 nestlings (1.4%) banded in the study area returned to nest the following year. This female fledged from a nest in 1998 at the mouth of South Creek. In 1999, she nested (unsuccessfully) along Nilumat Creek, 3,400 m distant. We have circumstantial evidence for natal philopatry for three birds (2 females, 1 male) banded as HYs during July 1997 which nested in the study area in 1998. These birds were not banded at the nest (which would have confirmed they were raised locally), but records during 1998 showed that at least 80% of birds captured during July (12 of 15) were recaptures known to have been raised within 1 km of the net array. A more plausible return rate

TABLE 3. Initial model testing for survival (S) of individually marked Eastern Yellow Wagtails nesting at Cape Romanzof, Alaska. Models are sorted by increasing AICc value. Subscripts reflect different factors in the model (t = year marked), g = group (juveniles or adult males). "t/." indicates year-dependence in that parameter for the first group and constancy in that parameter for the second group.

Model	p[a]	AIC_c[b]	ΔAIC_c	AIC weight[c]
S(g-t/.)	3	69.088	0.00	0.526
S(g*t)	4	69.532	0.44	0.421
S(g)	2	73.709	4.62	0.052
$S(g\text{-}a^2\ t/.)$	3	87.199	18.11	0.000
S(t)	2	104.372	35.28	0.000

[a] Number of estimated parameters.
[b] Akaike Information Criterion adjusted for small sample size.
[c] AIC weights calculated following Burnham and Anderson (1998).

for all 119 HYs banded was 3.6%. Thus, the minimum age of first breeding is 1 year.

One other locally-banded bird returned in 1998. An adult female captured in a mist net 100 m north of the mouth of Nilumat Creek on 8 August 1997 nested on lower Nilumat Creek in 1998. She may have nested nearby in 1997 but, when captured, she had no traces of a brood patch and had completed prebasic molt. We could not ascertain if the condition of this female's brood patch or molt was typical for a local breeder because no females known to have nested locally were captured in early August.

Annual Survival Estimates.—The most parsimonious models accounted for differences between both groups (adult male vs. juvenile) and years (Table 3). The model best supported by the data indicates variation among years for adult males but not juveniles. Survival estimates differed between years for both groups and between young and adult males. Apparent survival estimates (actual survival minus dispersal) were zero for adult females, because none returned to the study area. Apparent survival of adult males was 0.973 ± 0.0052 in 1998 and 0.386 ± 0.1057 in 1999. Apparent survival of juveniles was 0.044 ± 0.0232 in 1998 and 0.026 ± 0.0158 in 1999.

DISCUSSION

The demography of Eastern Yellow Wagtails at Cape Romanzof varied in our 3-year study and was characterized by relatively high adult male survival and site fidelity, female-biased dispersal, and weak natal philopatry. Apparent survival of adult males from 1997 to 1998 was more than double that in 1998–1999, and corresponded with a nearly proportional reduction in nesting attempts between those years (34 to 17 nests). We are confident that we had sufficient observations to detect any color-banded birds had they arrived in our study area. We could not assess the relative contributions of dispersal (perhaps resulting from habitat covered by snow) and mortality to the local population decline. However, Ashford (1970) and Wood (1976, 1979) reported high mortality (~50%) for Western Yellow Wagtails (*Motacilla flava*) in wintering areas in west Africa, as did McClure (1998) for Yellow Wagtails (*M. flava flavissima*) in Taiwan, due in large part to harvest by humans for food. If these rates apply to *M. tschutschensis*, and given the observed return rates (42–63%) of males banded at Cape Romanzof coupled with low natal philopatry, it is plausible that most males not re-observed at Cape Romanzof probably died rather than dispersed.

Eastern Yellow Wagtails at Cape Romanzof, relative to studies of wagtails in Europe, exhibited high male return/survival rates. Drost's (1948) 5-year banding study on Helgoland, Germany (54° 11′ N, 7° 55′ E, a 1-km^2 island, 45 km off the coast) documented return rates for Yellow Wagtails: 11 to 43% of banded birds returned after 1 year (5-year mean = 21%), and 7 to 22% of the original cohort (mean = 8%) returned after 2 years. Drost's data indicated that females returned in nearly equal proportions to males. No other published return rates are available for Yellow Wagtails although Martin and Clobert (1996) suggested European passerines (especially open-nesting species) have lower survival than their North American counterparts, balanced by higher fecundity. Indeed, Western Yellow Wagtails averaged >1 successful brood attempt each year (leading to higher overall fecundity despite a lower clutch size) while no wagtails at Cape Romanzof double-brooded (Renner and McCaffery 2006).

No nest-site-based data exist regarding fidelity of female Eastern or Western Yellow Wagtails at other locations (but see Paradis et al.1998 for calculated breeding and natal dispersal distances based on banding recoveries in Britain). The Paradis et al. (1998) study,

unlike our study, was designed to document large dispersal distances rather than precisely examine short distances between nests in subsequent years. However, the data from Paradis et al. (1998) fit with our results in suggesting breeding dispersal distances <1 km and substantially larger mean natal dispersal distances. Kovshar (1979) reported high philopatry among a small sample of female White Wagtails, where four of five females color-banded nested within 100 m of their previous year's nest and the other nested 1 km distant. One of 100 marked White Wagtail nestlings was recovered 2 years later, 300 m from its natal site, and seven more were recovered the following year, >1 km away (Kovshar 1979).

The demographic patterns we observed at Cape Romanzof (higher survival of males than females, and of adults than juveniles) generally fit with expectations for passerines. Greenwood (1980) showed that most bird species demonstrate female-biased breeding dispersal (i.e., females dispersed further than males after breeding), including 25 of 28 species and 14 of 15 families analyzed. The complete absence of returning females at Cape Romanzof (in contrast to the relatively high return rate of males) is extreme and warrants investigation into possible differences in migration stopovers and wintering locations.

Greenwood (1980) demonstrated that natal dispersal in birds is typically greater than breeding dispersal and is, as adult dispersal, also female-biased (i.e., females disperse further) in 21 of 24 species (11 of 12 families) examined. The small number of returning juveniles we observed matches the pattern reported by Greenwood (1980), but we did not find female-biased natal dispersal (3 of 4 returning fledglings were female). True juvenile survival is probably much higher than apparent survival. Ricklefs (1973) and Greenberg (1980) suggested that juvenile survival of most small land birds from fledging until return to breeding areas is 15–30%. Local survival estimates using mark-recapture data, as reported here, may significantly underestimate actual survival because juvenile dispersal is high in many species (Greenwood 1980).

Female passerines, particularly long-distance migrants, generally have higher mortality than males (Ricklefs 1973). Our data are consistent with this pattern but we consider it more plausible that our study population of Eastern Yellow Wagtails demonstrates a strong female bias in dispersal as well as mortality. If our estimate of adult female survival is representative, then observed fecundity rates are certainly too low to sustain this population without substantial and sustained immigration of females.

ACKNOWLEDGMENTS

We thank C. R. Smith, M. E. Richmond, and C. C. Krueger of the Department of Natural Resources at Cornell University for support throughout this project. Funding was provided by the U.S. Fish and Wildlife Service, Cornell University, Western Bird Banding Association, and a Walter Benning research grant. Logistical support at Cape Romanzof was provided by the PMC/Frontec staff. We thank the U.S. Air Force and particularly Gene Augustine (611th Air Support Group Conservation Resources Program, Elmendorf Air Force Base). The field work at Cape Romanzof would not have happened without their support and encouragement. Field data were collected by the authors, C. M. Harwood, M. E. Hopey, M. B. Krosby, Christine McCaffery, C. K. Melin, and A. M. Moreland. E. G. Cooch conducted the MARK survival analyses and provided substantial advice. Valuable comments on the manuscript were also provided by I. L. Jones, S. M. Matsuoka, Nadav Nur, Martin Renner, and B. K. Sandercock. Translation of German articles was provided by Harmony Hall.

LITERATURE CITED

Ashford, R. W. 1970. Yellow wagtails at a Nigerian winter roost: analysis of ringing data. Bulletin of Nigerian Ornithology 7:24–26.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. Biometrics 53:603–618.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference—a practical information-theoretic approach. Springer-Verlag, New York, USA.

Drost, V. R. 1948. Populationsstudien an der Englischen Schafstelze, *Motacilla flava flavissima* Blyth, auf Helgoland. Vogelwarte 1:18–28.

Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493–504 *in* Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, D.C., USA.

Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behavior 28:1140–1162.

Haas, C. 1990. Breeding ecology and site fidelity of American Robins, Brown Thrashers, and Loggerhead Shrikes in shelterbelts in North Dakota. Dis-

sertation. Cornell University, Ithaca, New York, USA.

Haas, C. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk 115:929–936.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

Klett, A. T., H. F. Duebbert, C. A. Faanes, and K. F. Higgins. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. USDI, Fish and Wildlife Service, Resource Publication 158. Washington, D.C., USA.

Kovshar, A. F. 1979. The singing birds of the subalpine belt of Tien Shan. Nauka, Alma-Ata, Kazakhstan.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Martin, T. E. and J. Clobert. 1996. Nest predation and avian life history evolution in Europe versus North America: a possible role of humans? American Naturalist 147:1028–1046.

Mayfield, H. F. 1960. Nest success calculated from exposure. Wilson Bulletin 73:255–261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

McClure, H. E. 1998. Migration and survival of the birds of Asia. White Lotus Co., Ltd, Bangkok, Thailand.

Michel, N., D. F. DeSante, D. R. Kaschube, and M. P. Nott. 2006. The Monitoring Avian Productivity and Survivorship (MAPS) Program annual reports, 1989–2003. NBII/MAPS Avian Demographics Query Interface. http://www.birdpop.org/nbii/NBIIHome.asp (accessed 18 December 2006).

Nichols, J. D., C. Brownie, J. E. Hines, K. H. Pollock, and J. B. Hestback. 1993. The estimation of exchanges among populations or subpopulations. Pages 264–280 *in* Marked individuals in the study of bird populations (J. D. Lebreton and P. M. North, Editors). Birkhauser-Verlag, Basel, Switzerland.

Nur, N. and W. J. Sydeman. 1999. Demographic processes and population dynamic models of seabirds. Current Ornithology 15:149–188.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns in natal and breeding dispersal in birds. Journal of Animal Ecology 67: 518–536.

Pollock, K. H., S. R. Winterstein, and M. J. Conroy. 1989a. Estimation and analysis of survival distributions for radio-tagged animals. Biometrics 45:99–109.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989b. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Renner, H. M. and B. J. McCaffery. 2006. Nesting biology of Eastern Yellow Wagtails at Cape Romanzof, Alaska. Journal of Field Ornithology 77: 1–9.

Ricklefs, R. L. 1973. Fecundity, mortality, and avian demography. Pages 366–435 *in* Breeding biology of birds (D. S. Farner, Editor). National Academy of Science, Philadelphia, Pennsylvania, USA.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.

Wood, B. 1976. The biology of Yellow Wagtails *Motacilla flava* L. overwintering in Nigeria. Dissertation. University of Aberdeen, Aberdeen, United Kingdom.

Wood, B. 1979. Changes in numbers of over-wintering Yellow Wagtail *Motacilla flava* and their food supplies in a West African savanna. Ibis 121:228–231.

The Wilson Journal of Ornithology 120(1):92–98, 2008

BREEDING ECOLOGY OF THE NARCISSUS FLYCATCHER IN NORTH CHINA

NING WANG,[1] YANYUN ZHANG,[1] AND GUANGMEI ZHENG[1,2]

ABSTRACT.—We studied the breeding ecology of the Narcissus Flycatcher (*Ficedula narcissina elisae*) in subalpine secondary broad-leaf forest near Beijing, China during 2003–2006. The Narcissus Flycatcher arrived in the breeding area at the beginning of May with first-spring males arriving later than older males. Nests of first-spring male Narcissus Flycatchers were at lower altitudes (1,271.0 ± 20.7 m) than those of older males (1,363.8 ± 22.5 m). Narcissus Flycatchers nested in diverse sites on different plant species with *Betula dahurica* being most commonly used. Nests of Narcissus Flycatchers were exposed and 2.5 ± 0.3 m above the ground with mean clutch size of 4.3 ± 0.2. Mean egg length was 17.2 ± 0.1 mm, mean egg width was 13.2 ± 0.1 mm. and mean egg mass was 1.5 ± 0.0 g. The mean incubation period was 13.4 ± 0.2 days and mean nestling period was 13.2 ± 0.2 days. Fledging success was 4.0 ± 0.3 fledglings per successful nest. The Narcissus Flycatcher had low breeding success (51.2%), mainly because of predation. *Received 28 November 2006. Accepted 16 July 2007.*

The Narcissus Flycatcher (*Ficedula narcissina*) is a gender-dimorphic small passerine that breeds in northeast Asia and winters in southeast Asia. One subspecies (*F. n. elisae*) breeds only in north China (Cheng 1987, Dickinson 2003, Zheng 2005) and was considered to be a distinct species based on morphological, acoustic, and molecular evidence (Weigold 1922, Li 2004, Zhang et al. 2006). This subspecies has delayed plumage maturation in first-spring males (Zhang et al. 2006). The plumage of first-spring males is similar to females instead of older males; these female-looking males sing like adult males and can breed successfully. The first-spring male was even mistakenly identified as a new species: *Ficedula beijingnica* (Zheng et al. 2000). Little information exists on the breeding ecology of *Ficedula narcissina elisae* and our objectives are to present data on the (1) reproductive phenology; (2) characteristics of nests, eggs, and nestlings; (3) reproductive behavior; and (4) breeding success of this subspecies.

METHODS

Study Area.—We studied Narcissus Flycatchers in the subalpine Xiao Longmen Forest (40° 00′ N, 115° 26′ E), 114 km west of Beijing, China. This forest is 705.4 ha in size at 1,000–1,763 m altitude. The terrain is rugged with steep slopes (30–60°) and the width of drainages ranges from 10 to 60 m. The mean annual temperature of the study area is ~4.8 °C and the annual precipitation is 500–700 mm. The vegetation is dominated by secondary temperate deciduous broad-leaf forest with patches of coniferous plantations. The broad-leaf forest is dominated by *Populus davidiana*, *P. cathayana*, *Salix viminalis*, *S. caprea*, *Juglans mandshurica*, *Betula platyphylla*, *B. dahurica*, *Quercus mongolica*, *Acer truncatum*, *Fraxinus rhynchophylla*, and *Syringa pekinensis*. Conifer plantations are dominated by *Larix principis-rupprechtii*, *L. kaempferi*, and *Pinus tabulaeformis*. Local people graze goats, cut firewood, and collect herbs, edible plants, and mushrooms in the forest. Our study site was 196.5 ha of largely broad-leaf trees in the southern part of the forest.

Nest-box Arrangement.—We erected 200 nest boxes (8.5 × 8.5 × 17.5 cm) in the study area from 2004 to 2006 before flycatchers arrived in spring. Half of the nest boxes had a large square entrance (9 × 8.5 cm) and the other half had a small round entrance (3.5-cm diam). Nest boxes were placed 3–4 m above ground on live tree trunks on both slopes of a drainage with entrances facing down slope. We collected data from May to July in 2004, 2005, and 2006 after a preliminary study from June to July 2003.

Breeding Surveys.—We searched for and

[1] College of Life Science, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Beijing Normal University, Beijing, 100875, China.

[2] Corresponding author;
e-mail: zhenggm@bnu.edu.cn

TABLE 1. Arrival dates of Narcissus and Yellow-rumped flycatchers in Xiao Longmen Forest, China.

	Narcissus Flycatcher			Yellow-rumped Flycatcher	
	Male				
Year	Older	First-spring	Female	Male	Female
2004	5 May	13 May	8 May	7 May	8 May
2005	3 May	15 May	6 May	6 May	9 May
2006	3 May	17 May	10 May	5 May	11 May

listened for songs of flycatchers every day each year starting on 1 May. After locating a bird, we tried to ascertain its species, gender, and age if it was a male. Older male Narcissus Flycatchers (≥2 years) have yellow superciliums, yellow rumps, and white patches on the greater coverts. First-spring males are without yellow superciliums and yellow rumps, and instead of white patches on greater coverts, they have two white wing bars. The date we found the first individual each year was used as the arrival date for that year.

Nests Searching and Monitoring.—We located nests by following adults displaying nesting behavior such as entering a hole or crevice, carrying plant fibers for nest-building, and taking invertebrates to feed nestlings, or we searched the vicinity of where adults were giving alarm calls. We monitored nests by recording date of the first egg, clutch size, date of hatching, date of fledging, and calculated reproductive success. Length, width, and mass of eggs were measured on day of laying. A breeding attempt was considered successful if at least one young fledged. We backdated egg-laying dates for nests found during incubation or after nestlings had hatched based on clutches with complete information. We calculated the duration between the arrival date and laying date of each clutch for statistical analyses.

Nest Site Characteristics.—We measured characteristics of nest sites after breeding ceased, including altitude, aspect, nesting tree species, height of the nest above ground, and dimension of the cavity where the nest was located. Characteristics of each nest site were included only once in statistical analyses even if the nest site was used several times in different years.

Statistical Analyses.—We used SPSS for Windows 11.0 for all analyses. The normality of data was examined using the one sample Kolmogorov-Smirov test. We compared means by *t*-tests for data with normal distribution and calculated Pearson's correlation coefficients. Equality of variances was tested by Levene's test. We used Mann-Whitney *U*-tests and Spearman's correlation coefficients for data that did not show normal distribution. Data are presented as $\bar{x} \pm$ SE, with maximum and minimum values. Significance was set at $P = 0.05$.

RESULTS

Arrival Dates.—Both Narcissus Flycatchers and Yellow-rumped Flycatchers (*Ficedula zanthopygia*) occurred on our study area. Narcissus Flycatchers arrived in the beginning of May with males arriving 3–7 days earlier than females, while first-spring males arrived 8–12 days later than older males. Yellow-rumped Flycatchers arrived 2–3 days later than Narcissus Flycatchers and males arrived 1–6 days earlier than females (Table 1).

Nest Site Characteristics.—We found 43 Narcissus Flycatcher nests, 2 in 2003, 17 in 2004, 7 in 2005, and 17 in 2006. Fourteen nests were found during nest-building, 5 during egg-laying, 12 during incubation, 5 during the nestling stage, and 7 just after fledging when parents were still feeding their young nearby. Seven nests had first-spring males. Narcissus Flycatchers nested in tree forks formed by upward reaching branches (10 nests), hollows at the top of stakes (11 nests), cavities on tree trunks (13 nests), and in nest boxes with larger square entrances (9 nests). Both first-spring and older males used the four types of nest-sites with no difference detected between age groups (Chi-square test, $\chi^2 = 2.525$, df = 3, $P = 0.471$). None of the nest boxes with small round entrances was used by Narcissus Flycatchers. Some nest sites were used repeatedly: one cavity in a tree trunk was used in 2003, 2004, and 2006; another cavity in a tree trunk was used in 2004 and 2006;

one hollow at the top of a stake was used in 2004 and 2006.

We found 27 Yellow-rumped Flycatcher nests, 4 in 2003, 7 in 2004, 7 in 2005, and 9 in 2006. Nine nests were found during nest-building, 2 during egg-laying, 10 during incubation, and 6 during nestling stages. Yellow-rumped Flycatchers nested in cavities in tree trunks (11 nests), nest boxes with small round entrances (15 nests), and one nest was in a cavity on a brick wall. None of the nest boxes with larger square entrances was used by Yellow-rumped Flycatchers. One cavity in a tree trunk was used in 2003 and 2004. Cavities in tree trunks used as nest sites by Yellow-rumped Flycatchers significantly differed from those used by Narcissus Flycatchers both in the smallest diameter (Yellow-rumped Flycatcher: 4.6 ± 0.3 cm, range = 4.0–6.0 cm, n = 10; Narcissus Flycatcher: 6.7 ± 0.5, range = 3.5–8.0 cm, n = 9: Mann-Whitney U-test, $Z = -2.583$, $P = 0.010$) and in the largest diameter (Yellow-rumped Flycatcher: 5.5 ± 0.6 cm, range = 4.0–9.0 cm, n = 10; Narcissus Flycatcher: 18.5 ± 6.9, range = 5.0–72.0 cm, n = 9; Mann-Whitney U-test, $Z = -3.052$, $P = 0.002$).

Narcissus Flycatchers nested at higher elevation (1,347.1 ± 19.6 m, range = 1,150–1,577 m, n = 39) than Yellow-rumped Flycatchers (1,237.0 ± 21.8 m, range = 1,070–1,473 m, n = 26; Independent-samples t-test: $t = 3.688$, df = 63, $P < 0.001$). First-spring male Narcissus Flycatchers nested at lower elevation than older males (first-year males: 1,271.0 ± 20.7 m, range = 1,173–1,350 m, n = 7; older males: 1,363.8 ± 22.5 m, range = 1,150–1,577 m, n = 32; Independent-samples t-test: $t = -3.032$, df = 37, $P = 0.006$).

Twenty-five of 39 Narcissus Flycatcher nests were on north-facing slopes, 5 were on south-facing slopes, and 9 were in drainages (Chi-square test, $\chi^2 = 17.231$, df = 2, $P < 0.001$). First-spring males nested on north-facing slopes (n = 4) and in drainages (n = 3). Twelve of 26 Yellow-rumped Flycatcher nests were on north-facing slopes, 3 were on south-facing slopes, and 11 were in drainages (Chi-square test, $\chi^2 = 5.615$, df = 2, $P = 0.060$). No difference (Chi-square test, $\chi^2 = 5.517$, df = 1, $P = 0.063$) was detected between Yellow-rumped and Narcissus flycatchers in slopes chosen for nesting.

Narcissus Flycatchers nested lower above ground (2.5 ± 0.3 m, range = 0.4–8.0 m, n = 39) than Yellow-rumped Flycatchers (4.2 ± 0.3 m, range = 2.2–7.0 m, n = 26; Independent-samples t-test, $t = -4.299$, df = 63, $P < 0.001$). Nests of first-spring male Narcissus Flycatchers were at the same height as older males (Independent-samples t-test, $t = -0.604$, df = 37, $P = 0.55$).

Narcissus Flycatchers nested on nine plant species (Table 2), with 20 of 39 nests on *Betula dahurica* (Chi-square test, $\chi^2 = 67.846$, df = 8, $P < 0.001$). First-spring males nested on five plant species with these species used also by older males. Sixteen of 39 Narcissus Flycatcher nests were on dead trees or stakes (Chi-square test, $\chi^2 = 1.256$, df = 1, $P = 0.26$). One of seven nests of first-spring males was on a stake with no difference (Chi-square test, $\chi^2 = 0.2.982$, df = 1, $P = 0.084$) detected between age groups.

Yellow-rumped Flycatchers also nested on nine plant species (Table 2), but only three of these species (*Juglans mandshurica*, *Betula platyphylla*, and *B. dahurica*) were used by Narcissus Flycatchers. Nine of 25 nests of Yellow-rumped Flycatcher (excluding the nest on brick wall) were on dead trees (Chi-square test, $\chi^2 = 1.960$, df = 1, $P = 0.16$), not different (Chi-square test, $\chi^2 = 0.262$, df = 1, $P = 0.608$) from that recorded for the Narcissus Flycatcher.

Egg-laying, Clutch Size, and Egg Characteristics.—The earliest Narcissus Flycatcher clutch was laid in the second half of May and the latest was laid in the beginning of July. We could not confirm whether second clutches were laid after completion or failure of the first nesting attempt in a breeding season. The mean duration between the arrival date of Narcissus Flycatchers and date of the first egg of every clutch that year was 34.3 ± 2.5 days (range = 16–54 days, n = 21). The mean clutch size of Narcissus Flycatcher was 4.3 ± 0.2 (range = 3–6, n = 19). Two clutches had 3 eggs, 10 had 4 eggs, 6 had 5 eggs, and 1 had 6 eggs. Clutch size of first-spring males did not differ from that of older males (Independent-samples t-test, $t = -0.192$, df = 17, $P = 0.85$). There was a negative correlation between clutch size and date of the first egg

TABLE 2. Plants used by Narcissus and Yellow-rumped flycatchers for nesting in Xiao Longmen Forest, China.

Plant species	Narcissus Flycatcher			Yellow-rumped Flycatcher		
	Live trees	Dead trees	Totals	Live trees	Dead trees	Totals
Pinus tabulaeformis	2		2			
Populus davidiana				2	1	3
P. cathayana				2		2
Salix viminalis				3	1	4
S. caprea	1	5	6			
Juglans mandshurica		2	2	7		7
Betula platyphylla	1	2	3	2		2
B. dahurica	15 (3)[a]	5	20 (3)	1	1	2
Corylus mandshurica	1 (1)		1 (1)			
Ulmus laciniata				1		1
U. propinqua	2 (1)		2 (1)			
Malus baccata					1	1
Acer truncatum		2 (1)	2 (1)			
Fraxinus rhynchophylla					1	1
Syringa pekinensis				1	1	2
Abelia biflora	1 (1)		1 (1)			

[a] Numbers of nests of first-spring male Narcissus Flycatchers.

(Pearson's correlation coefficient $r = -0.748$, $P < 0.001$). The color of Narcissus Flycatcher eggs ranged from whitish pink to light blue with rusty speckles. Mean egg length was 17.2 ± 0.1 mm (range = 14.8–18.6 mm, $n = 38$) with mean width of 13.2 ± 0.1 mm (range = 12.0–13.8 mm, $n = 38$). The mean mass of Narcissus Flycatcher eggs was 1.5 ± 0.0 g (range = 1.2–1.7 g, $n = 23$).

The mean clutch size of Yellow-rumped Flycatchers was 4.8 ± 0.2 (range = 4–6, $n = 10$). Three of the clutches had four eggs, six had five eggs, and one had six eggs. The clutch size of Yellow-rumped Flycatchers did not differ (Independent-samples t-test, $t = -1.740$, df = 27, $P = 0.093$) from that of Narcissus Flycatchers. The color of Yellow-rumped Flycatcher eggs was similar to that of Narcissus Flycatcher eggs. Mean egg length was 17.1 ± 0.2 mm (range = 15.0–17.9 mm, $n = 16$) and mean width was 13.1 ± 0.1 mm (range = 12.8–13.5 mm, $n = 16$). Neither measurement differed (Independent-samples t-test, $t = 0.495$, df = 52, $P = 0.62$ for length; $t = 0.661$, df = 52, $P = 0.51$ for width) from those of Narcissus Flycatchers. The mean mass of Yellow-rumped Flycatcher eggs was 1.4 ± 0.0 g (range = 1.1–1.6 g, $n = 15$), slightly less than those of Narcissus Flycatchers (Independent-samples t-test, $t = 2.824$, df = 36, $P = 0.008$).

Incubation and Parental Care.—Incubation of Narcissus Flycatcher nests was by the female alone and males were observed feeding their incubating mate. Some females initiated incubation before their clutches were complete and this most likely led to asynchronous hatching (within 2 days) observed in several clutches. The mean incubation period was 13.4 ± 0.2 days (range = 12–14 days, $n = 17$). Length of incubation was negatively correlated to laying date (Pearson's correlation coefficient, $r = -0.499$, $P = 0.049$) and positively with clutch size (Pearson's correlation coefficient, $r = 0.699$, $P = 0.002$). Mean survival of nests to hatching was 0.91 ± 0.04 (range = 0.60–1.00, $n = 17$). Mean hatching success was 3.9 ± 0.2 nestlings (range = 2–6 nestlings, $n = 17$) with brood size positively correlated to clutch size (Pearson's correlation coefficient, $r = 0.637$, $P = 0.008$). There was no difference between nests of first-spring versus older males in incubation periods, survival of nests to hatching, and hatching success (Independent-samples t-test, all $P > 0.05$).

Both male and female Narcissus Flycatcher fed their young. The mean nestling period was 13.2 ± 0.2 days (range = 12–14 days, $n = 13$). Length of nestling period correlated negatively to laying date (Spearman's correlation coefficient, $r = -0.657$, $P = 0.015$) and pos-

itively to brood size (Spearman's correlation coefficient, $r = 0.853$, $P < 0.001$). All nestlings from the same clutch fledged in the same morning. Fledging success was 4.0 ± 0.3 fledglings (range = 3–6 fledglings, $n = 13$) per successful nest. There was no difference (Mann-Whitney *U*-test, all $P > 0.05$) between first-spring and older males in nestling periods and numbers of fledglings per successful nest.

Breeding Success.—Twenty-two of 43 Narcissus Flycatcher nests in Xiao Longmen Forest successfully fledged young, and the proportion of successful and failing nests was nearly the same (Chi-square test, $\chi^2 = 0.023$, df = 1, $P = 0.88$). Three of seven nests of first-spring males succeeded and the proportion of successful nests did not differ from that of older males (Chi-square test, $\chi^2 = 0.281$, df = 1, $P = 0.596$). Five nests failed during nest-building, 4 during egg-laying, 6 during incubation, and 6 during the nestling stage. Predation accounted for failure of 17 nests. Likely predators included Swinhoe's striped squirrel (*Tamiops swinheoi*), rock squirrel (*Sciurotamias davidianus*), Siberian weasel (*Mustela sibirica*), Japanese Sparrowhawk (*Accipiter gularis*), Great Spotted Woodpecker (*Picoides major*), Eurasian Jay (*Garrulus glandarius*), Red-billed Blue Magpie (*Urocissa erythrorhyncha*), and Chifeng beauty snake (*Elaphe anomala*). Other causes for nest failure were storms (2 nests), human disturbance (1 nest), and ants taking over the cavity (1 nest) after an egg was laid.

Twenty of 27 nests of Yellow-rumped Flycatcher in Xiao Longmen Forest successfully fledged young and the proportion of successful nests was higher than that of failing nests (Chi-square test, $\chi^2 = 6.259$, df = 1, $P = 0.012$). Yellow-rumped Flycatchers had higher breeding success than Narcissus Flycatcher (Chi-square test, $\chi^2 = 5.679$, df = 1, $P = 0.017$). Four nests failed during nest-building, 1 during egg-laying, 1 during incubation, and 1 during the nestling stage. Two nests were depredated, 2 were destroyed by humans, 1 was taken over by wasps during the nest-building stage, 1 was destroyed by a storm, and 1 was abandoned after an egg was laid.

Molt.—Fledgling Narcissus flycatchers were olive green with light yellow speckles on the dorsal side and light yellow with olive green streaks on the ventral side. Remiges were olive brown, and wing coverts were olive brown with light yellow tips, which formed horizontal bars on greater and middle coverts. Rectrices were olive brown. Fledglings began their post-natal molt about a month after fledging. Remiges, wing coverts, and rectrices were not involved in this molt. The post-natal molt ended at the beginning of September. Juvenile males and females were alike in plumage, both olive green above and light yellow below.

Males which returned to the breeding area in their second calendar year (first-spring) still looked like females. First-spring males began their first postnuptial molt at the end of June when their contour feathers, remiges, wing coverts, and rectrices went through a complete molt. Primaries molted descendantly and secondaries molted ascendantly. Rectrices molted centrifugally. Males obtained their typical adult plumage in early September of their second calendar year with head to back olive green and with yellow superciliums and rump. The underparts were yellow, remiges and wing coverts were blackish brown with white patches on greater coverts, and rectrices were blackish brown. Female plumage color did not change noticeably after their first postnuptial molt.

DISCUSSION

Arrival Dates.—Older Narcissus Flycatcher males arrived earlier than young males similar to European Pied Flycatchers (*Ficedula hypoleuca*) (Potti and Montalvo 1991, Potti 1998a), Collared Flycatchers (*F. albicollis*) (Mitrus et al. 1996, Mitrus 2004), and Red-breasted Flycatchers (*F. parva*) (Mitrus 2006, Mitrus et al. 2006). Delayed settlement of young males may result from delayed departure from wintering areas or delayed maturation. Males which bred in previous seasons return to their known breeding places (Pärt and Gustaffsson 1989) while young males may have to spend time searching for suitable breeding sites.

Male Narcissus and Yellow-rumped flycatchers both arrived earlier than females similar to Pied, Collared, and Red-breasted flycatchers (Dement'ev and Gladkov 1968). This suggests pair bonding in both species occurred after arrival in breeding areas. We observed males of both Narcissus and Yellow-rumped flycatchers displaying to females by going in

and out of their nest holes followed by the females entering the holes to inspect the nest sites similar to that reported for European Pied Flycatcher (Rinden et al. 1995). This type of nest-site display suggests that quality of the nest site occupied by a male is an important criterion in mate selection.

Nest Sites Characteristics.—Narcissus Flycatchers nested at higher altitudes than Yellow-rumped Flycatchers in Xiao Longmen Forest indicating separation in habitat use by elevation. Narcissus Flycatchers near Beijing bred in subalpine forest while Yellow-rumped Flycatchers bred in low elevation woodlands (Zheng 1984, Cai 1987). Replacement of congeners by elevation was observed in other passerines near Beijing (Zheng 1984) including Marsh (*Poecile palustris*) and Willow tits (*P. montana*), Meadow (*Emberiza cioides*) and Godlewski's buntings (*E. godlewskii*), Black (*Dicrurus macrocercus*) and Hair-crested drongos (*D. hottentottus*), and White-throated (*Monticola gularis*) and Blue Rock thrushes (*M. solitarius*). Breeding habitat of Narcissus Flycatchers in our study, where the two flycatchers were sympatric, was dominated by *Betula dahurica* while the breeding habitat of Yellow-rumped Flycatcher was dominated by *Juglans mandshurica* (Wang et al. 2006). This implies partitioning in microhabitat use by the two species when they were sympatric.

Narcissus Flycatchers used more diverse and exposed nest sites closer to the ground than those used by Yellow-rumped Flycatchers and other typical secondary hole-nesting passerines such as tits (*Poecile* spp.) and nuthatches (*Sitta* spp.) that bred sympatricly in Xiao Longmen Forest. This is similar to sympatricly-breeding Red-breasted and European Pied flycatchers, and other secondary cavity nesters in Poland (Mitrus and Soćko 2004) where Red-breasted Flycatchers used more open, lower, and more diverse-shaped nest cavities than other species. In Europe, European Pied Flycatchers nested in higher holes with smaller entrances in trees than sympatricly breeding Collared Flycatchers (Czeszczewik and Walankiewicz 2003).

The separation between Narcissus and Yellow-rumped flycatchers in nest sites could be affected by inter-specific conflicts. We observed male Yellow-rumped Flycatchers expel male Narcissus Flycatchers near nest sites of the former, suggesting Yellow-rumped Flycatchers are dominant in inter-specific conflicts. Accepting diverse nest sites could maximize the possibility that subdominant Narcissus Flycatchers may breed. Lower breeding success of Narcissus Flycatchers suggested that subdominant species may use suboptimal nest sites.

Breeding Behaviors and Reproductive Parameters.—Late breeding Narcissus Flycatcher pairs had smaller clutches, shorter hatching periods, fewer nestlings, and shorter nestling periods than pairs that bred early. This is consistent with patterns reported for European Pied Flycatchers breeding in temperate areas (Jarvinen and Vaisanen 1983, Alatalo and Lundberg 1984, Moreno and Carlson 1989, Sanz 1996, Eeva et al. 2000). Short breeding seasons in temperate subalpine areas such as Xiao Longmen Forest compel breeding birds to complete their reproductive cycle within a short time, particularly for late breeders. Most passerines that breed in Xiao Longmen Forest fledge their young before late July.

Male Narcissus Flycatcher fed their mates during incubation and brooding. This was also reported for European Pied Flycatchers (Sanz 1996). Male provisioning could decrease the frequency and duration when a female was absent from the nest (Moreno and Carlson 1989), so that continuous warming of the eggs was possible. In subalpine areas with low temperatures near dawn, such as in Xiao Longmen Forest, it may be important that females remain on their nests.

Asynchronous hatching within a Narcissus Flycatcher clutch is similar to European Pied Flycatchers (Potti 1998b). The proportion of asynchronous hatching for European Pied Flycatchers was higher in better habitat and milder weather than in poor habitat or severe weather (Slagsvold 1986, Slagsvold and Lifjeld 1989). It also varied with apparent quality of the female (Potti 1998b).

ACKNOWLEDGMENTS

We thank the managers of Xiao Longmen Forest for accommodation, J. Zhang, Y. Sun, Q. L. Ma, and L. Dong for field assistance. We also thank L. L. Severinghaus for improving the English of the draft, editor C. E. Braun for proofreading the English of the manuscript, and two anonymous reviewers for commenting on the manuscript. Financial support was provided by

National Sciences Foundation of China (Grant 30170115).

LITERATURE CITED

ALATALO, R. V. AND A. LUNDBERG. 1984. Density-dependence in breeding success of the Pied Flycatcher (*Ficedula hypoleuca*). Journal of Animal Ecology 53:969–977.

CAI, Q. K. 1987. Birds of Beijing. Beijing Press, Beijing, China.

CHENG, T. H. 1987. A synopsis of avifauna of China. Science Press, Beijing, China.

CZESZCZEWIK, D. AND W. WALANKIEWICZ. 2003. Natural nest sites of the Pied Flycatcher *Ficedula hypoleuca* in a primeval forest. Ardea 91:221–229.

DEMENT'EV, G. P. AND N. A. GLADKOV. 1968. Birds of the Soviet Union. Volume 4. Israel Program for Scientific Translations Ltd., Jerusalem, Israel.

DICKINSON, E. 2003. The Howard and Moore complete checklist of the birds of the world. Third Edition. Christopher Helm, London, United Kingdom.

EEVA, T., S. VEISTOLA, AND E. LEHIKOINEN. 2000. Timing of breeding in subarctic passerines in relation to food availability. Canadian Journal of Zoology 78:67–78.

JARVINEN, A. AND R. A. VAISANEN. 1983. Egg size and related reproductive traits in a southern passerine *Ficedula hypoleuca* breeding in an extreme northern environment. Ornis Scandinavica 14:253–262.

LI, W. 2004. Studies on the molecular phylogeny and taxonomic status of part of the genus *Ficedula*. Thesis. Beijing Normal University, Beijing, China.

MITRUS, C. 2004. No effect of age of males on reproductive success of the Collared Flycatcher *Ficedula albicollis*. Folia Zoologica 53:319–328.

MITRUS, C. 2006. The influence of male age and phenology on reproductive success of the Red-breasted Flycatcher (*Ficedula parva* Bechst.). Annales Zoologici Fennici 43:358–365.

MITRUS, C. AND B. SOĆKO. 2004. Natural nest sites of the Red-breasted Flycatcher *Ficedula parva* in a primeval forest. Acta Ornithologica 39:53–57.

MITRUS, C., N. KLESZKO, AND B. SOCKO. 2006. Habitat characteristics, age, and arrival date of male Red-breasted Flycatchers *Ficedula parva*. Ethology, Ecology and Evolution 18:33–41.

MITRUS, C., W. WALANKIEWICZ, D. CZESZCZEWIK, AND P. M. JABŁOŃSKI. 1996. Age and arrival date of Collared Flycatcher *Ficedula albicollis* males do not influence quality of natural cavities used. Acta Ornithologica 31:101–106.

MORENO, J. AND A. CARLSON. 1989. Clutch size and the costs of incubation in the Pied Flycatcher *Ficedula hypoleuca*. Ornis Scandinavica 20:123–128.

PÄRT, T. AND L. GUSTAFSSON. 1989. Breeding dispersal in the Collared Flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. Journal of Animal Ecology 58:305–320.

POTTI, J. 1998a. Arrival time from spring migration in male Pied Flycatchers: individual consistency and familial resemblance. Condor 100:702–708.

POTTI, J. 1998b. Variation in the onset of incubation in the Pied Flycatcher (*Ficedula hypoleuca*): fitness consequences and constraints. Journal of Zoology 245:335–344.

POTTI, J. AND S. MONTALVO. 1991. Male arrival and female mate choice in Pied Flycatchers *Ficedula hypoleuca* in central Spain. Ornis Scandinavica 22:45–54.

RINDEN, H., S. DALE, AND T. SLAGSVOLD. 1995. Male display behaviour and the assessment of male quality during visits by female Pied Flycatchers *Ficedula hypoleuca*. Fauna Norvegica, Series C: Cinclus 18:107–117.

SANDZ, J. J. 1996. Effect of food availability on incubation period in the Pied Flycatcher (*Ficedula hypoleuca*). Auk 113:249–253.

SLAGSVOLD, T. 1986. Asynchronous versus synchronous hatching in birds: experiments with the Pied Flycatcher. Journal of Animal Ecology 55:1115–1134.

SLAGSVOLD, T. AND J. T. LIFJELD. 1989. Constraints on hatching asynchrony and egg size in Pied Flycatchers. Journal of Animal Ecology 58:837–849.

WANG, N., Y. Y. ZHANG, AND G. M. ZHENG. 2006. Home ranges and habitat vegetation characters in breeding season of Narcissus Flycatcher and Yellow-rumped Flycatcher. Journal of Beijing Normal University (Natural Science) 42:295–299.

WEIGOLD, H. 1922. *Muscicapa elisae* n. sp. Falco 18: 1–2.

ZHANG, Y. Y., N. WANG, J. ZHANG, AND G. M. ZHENG. 2006. Acoustic difference of Narcissus Flycatcher complex. Acta Zoological Sinica 52:648–654.

ZHENG, G. M. 1984. Ecological distribution of birds in Beijing and its vicinity during summer. Chinese Zoological Research 5:29–40.

ZHENG, G. M. 2005. A checklist on the classification and distribution of the birds of China. Science Press, Beijing, China.

ZHENG, G. M., J. SONG, Z. W. ZHANG, Y. Y. ZHANG, AND D. S. GUO. 2000. A new species of flycatcher *Ficedula* from China (Aves: Passeriformes-Muscicapidae). Journal of Beijing Normal University (Natural Science) 36:405–409.

The Wilson Journal of Ornithology 120(1):99–104, 2008

REPRODUCTIVE SUCCESS OF HOUSE WRENS IN SUBURBAN AND RURAL LANDSCAPES

MICHAEL J. NEWHOUSE,[1,2,4] PETER P. MARRA,[1,3] AND L. SCOTT JOHNSON[2]

ABSTRACT.—We investigated the impacts of urbanization on reproductive success of House Wrens (*Troglodytes aedon*). We compared reproductive effort and success for 33 nesting attempts in suburban sites (2.5–10 buildings/ha) and 43 nesting attempts in rural sites (<2.5 buildings/ha) in and around the Washington, D.C.–Baltimore, Maryland, metropolitan area. There were no differences in clutch initiation dates or clutch sizes between suburban and rural nests. However, nestlings at suburban nests weighed less and had smaller body size prior to fledging compared to nestlings at rural nests. Parental feeding rates differed between suburban and rural nests during the "early nestling stage" (day 3 to day 6), but not in the "late nestling stage" (day 8 to day 12) suggesting average quality of prey for nestlings may be lower at suburban sites. Overall, suburban nests fledged more young than rural nests largely because of higher rates of nest predation on rural nests. Further research on how food availability and predation affects nesting success of House Wrens and other birds along urbanization gradients may provide important insights into impacts of urbanization on birds. *Received 1 November 2006. Accepted 1 April 2007.*

Land development can directly or indirectly impact native bird populations. For example, development alters habitat thereby reducing available areas for breeding and associated activities. Developed areas can have higher levels of human disturbance (Geise 1996, Beale and Monaghan 2004) and more chemical contaminants than rural areas (Obendorf et al. 2006; K. E. Roux and P. P. Marra, pers. comm.), which can indirectly impact birds through ingestion of contaminated food (e.g., fruit, phytophagous insects). Native bird species often rely on structurally complex habitats with a high proportion of native vegetation for nest sites and food making them particularly vulnerable in developed areas where invasive species often dominate and vegetation structure has been changed drastically (Goldstein et al. 1986, Mills et al. 1991, Case 1996, Pavlik and Pavlik 2000, Hennings and Edge 2003). Finally, as natural areas become fragmented by urbanization the percentage of edge versus interior habitat also increases resulting in birds nesting in edge habitats experiencing higher rates of nest predation (Robinson et al. 1995, Donovan et al. 1997, Donnelly 2002, Donnelly and Marzluff 2004).

Despite the challenges that affect birds in developed environments, habitats in urban/suburban areas may attract birds by presenting them with historically reliable cues to suitable nesting habitat. Patches of apparently suitable breeding habitat that remain in developed environments may become "ecological traps" (i.e., habitats that lure birds to settle, but result in lower overall fitness) (Gates and Gysel 1978, Purcell and Verner 1998, Donovan and Thompson 2001, Kokko and Sutherland 2001, Schlaepfer et al. 2002, Weldon and Haddad 2005). Developed areas may be population sinks—areas occupied by breeding birds but with individuals producing too few surviving young to sustain the local population (e.g., Misenhelter and Rotenberry 2000, Resumeš 2000).

Few studies have examined the impacts of urbanization on bird reproductive success and on individual fitness. Most research has examined how rates of nest depredation vary along urban to rural land-use gradients or with increasing forest fragmentation (e.g., Robinson et al. 1995, Patten and Bolger 2003). The general conclusion from these studies is that depredation increases with proximity to forest edge. Leston and Rodewald (2006) examined reproductive success of Northern Cardinals (*Cardinalis cardinalis*) in forests within urban and suburban land-use types; they found these sites provided suitable breeding habitat and

[1] Smithsonian Environmental Research Center, Edgewater, MD 21037, USA.

[2] Department of Biological Sciences, Towson University, Towson, MD 21252, USA.

[3] Current address: Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C. 20008, USA.

[4] Corresponding author; New Jersey Meadowlands Commission, Lyndhurst, NJ 07071, USA; e-mail: michael.newhouse@njmeadowlands.gov

were not ecological traps. However, response to the effects of urbanization may vary between species.

We examined the reproductive success of House Wrens (*Troglodytes aedon*) nesting in the rural and suburban habitat matrix. Our primary objective was to ascertain whether suburban development negatively impacted reproductive success of this cavity-nesting species. House Wrens are well-suited for study of the impacts of development on reproductive success because they prefer open woodlands and readily nest in suburban areas.

METHODS

Study Species.—House Wrens are small (10–12 g), migratory, insectivorous, secondary cavity-nesting songbirds that breed across much of North America (Johnson 1998). This species nests naturally in pre-formed tree cavities but readily uses nest boxes. Females normally produce two broods each season, laying 6–8 eggs for first breeding attempts and 4–7 eggs for second attempts. Only females brood young but both adults feed nestlings.

Study Sites and Nest Box Examination.—We conducted this study during spring and summer 2004 in and around the Washington, D.C.–Baltimore, Maryland, metropolitan area. The Washington, D.C. area has experienced a five-fold increase in human population density during the last century from 1.1 million residents in 1900 to approximately 5.3 million in 2000 (Negative Population Growth 2005).

In this study, 202 of 210 nest boxes available to wrens were on properties (i.e., yards) owned by participants in the Neighborhood Nestwatch Program. This project is operated by the Smithsonian Migratory Bird Center (SMBC) of the National Zoological Park (http://www.fonz.org/nestwatch.htm). We classified properties as suburban or rural based on the density of human dwellings in the area surrounding a nest site (Cam et al. 2000, Marzluff 2001, Thorington and Bowman 2003). We followed Marzluff (2001) and classified the habitat surrounding a nest as suburban if it had 2.5–10 dwellings/ha and rural if there were $\leq$2.5 dwellings/ha.

Several landowners had existing nest boxes and we added 65 additional nest boxes to properties prior to start of our study, distributing them equally between suburban and rural habitats. All added nest boxes were suspended from trees approximately 2.5–3.0 m above ground and were not equipped with predator deterrent devices. Ultimately, each site contained an average of three nest boxes. Of the eight nests that were not part of the Nestwatch program, seven were at environmental education centers in rural Maryland while one was in a suburban neighborhood. Three of 91 boxes (3%) in suburban habitats and 83 of 119 boxes (69%) in rural habitats had predator deterrent devices.

We checked nest boxes every 4–5 days beginning in mid-April until males present had paired. Thereafter, we visited each nest every other day to identify dates on which the first eggs were laid (all dates are reported as Julian dates). Female House Wrens usually lay one egg/day. We captured adults with mist nets and marked them with a USGS numbered aluminum leg band and two colored bands. Males were captured after pairing. Females were not captured until their eggs had hatched to reduce risk of nest abandonment. No nests were abandoned immediately after female capture.

We visited nest boxes 7–10 days after the first egg was laid to measure clutch size. We did not check nests daily after laying began and could not compare rates of partial clutch loss in suburban and rural habitats. We checked nests daily starting 11 days after laying ended to identify the day that hatching began. We termed the date of hatching Nestling Stage Day (NSD) 0. We banded, weighed nestlings, and measured both their wing chord and tarsus to the nearest 0.01 mm on NSD 11.

We recorded the number of young fledged from a nest as the number of young present on NSD 11 minus the number of young found dead in the nest after fledging. We considered a nesting attempt successful if $\geq$1 nestling fledged from the nest. All nests that failed appeared to do so as a result of abandonment, depredation, conspecific nest destruction, or hypothermia. There were no nests in which nestlings disappeared gradually or as a result of apparent starvation. We assumed parental abandonment when eggs were present but unattended. We assumed abandonment or hypothermia when all nestlings were found dead in the nest. We assumed predation when eggs or nestlings were missing and nest contents

were substantially disturbed. We also assumed predation when nest contents were not disturbed, eggs or young had disappeared, and the nest had not been occupied by a new male. Finally, we assumed conspecific nest destruction had occurred when the nest was largely intact, all eggs or nestlings were missing from the nest, and a new male had occupied the nest.

Parental Provisioning Behavior.—We recorded the number of trips made by parents to deliver food to nestlings for one continuous hour between the 0700 and 1100 hrs EST. We monitored nests with binoculars from a distance of 15–20 m. Data collection began when both parents appeared to be accustomed to our presence (typically about 5 min). We documented provisioning rates at two points during the nestling stage, "early" (NSD 2 to NSD 6, $n = 16$) and "late" (NSD 8 to NSD 12, $n = 24$). Some nests ($n = 11$) were observed during both early and late nestling stages. Adults typically deliver a single prey item per trip; thus, the number of provisioning trips generally equals the number of prey items transported to the nest (Morrison and Johnson 2002). We also documented the total time that females spent brooding young. We assumed that time in the nest box >1 min involved brooding. All observations were at a similar time of season.

We observed two parents provisioning nestlings at most nests during the early nestling stage including 9 of 10 suburban and 7 of 11 rural nests. Only females were provisioning at the remaining nests. In contrast, we observed only one parent provisioning at 10 of 15 suburban nests (eight females, two males) and 9 of 10 rural nests (seven females, two males) during the latter part of the nestling stage. Desertion of the nest by one parent, usually the male, is not uncommon in House Wrens (Czapka and Johnson 2000). Our intent was to use provisioning rates as an index of prey availability as the number of parents provisioning at a nest will influence feeding rates. Thus, we included only those early stage observations in which two parents were provisioning and only those late-stage observations with only one parent provisioning in our analysis.

Statistical Analyses.—We compared the mean date the first egg was laid in the first 15 nests of the season in the two habitat types using a *t*-test to examine whether onset of breeding differed in suburban and rural habitats. We used analysis of covariance (ANCOVA) with date of first egg as a covariate to compare clutch size. We report least-squares means adjusted for effects of laying date. We used the same analysis to compare the number of young fledged from successful nests. We could not use ANCOVA to compare number of young fledged from all nests, successful and unsuccessful, because data were not normally distributed. Therefore, we compared numbers of fledglings from all nests using a Wilcoxon Rank Sum test. We used the same test to compare number of fledglings per egg laid. We compared measures of nestling mass and size using a *t*-test, using mean brood values to avoid pseudoreplication. Broods tended to be smaller in rural nests and we also compared nestling measures using ANCOVA with brood size as a covariate and report least-squares means adjusted for brood size. We report interactions only if significant. We report means ± SE unless otherwise noted. All statistical analyses were performed using SAS Version 8.1 (SAS Institute 1999).

RESULTS

We monitored reproduction at 76 nests (Table 1), 33 in suburban areas (17 first and 16 second broods) and 43 in rural habitats (24 first and 19 second broods). Birds in suburban and rural areas commenced breeding at the same time and laid similarly sized clutches. However, House Wrens in rural habitats were less successful ($P < 0.001$) at fledging at least one nestling than those in suburban habitats (60 vs. 88% of nests, respectively). Seven of the 17 (41%) unsuccessful nests in rural habitats were most likely destroyed by snakes and the remaining 10 were either destroyed by predators or by conspecifics. We could not clearly assign cause of failure in two of the four cases where nests failed in suburban habitats. In the remaining two cases, the entire brood was found dead suggesting either abandonment or death from hypothermia. A greater proportion of nests in rural compared to suburban habitats were destroyed by predators (0 vs. 41%; $\chi^2 = 3.69$, $P = 0.05$). This explains, in part, why rural nests fledged significantly fewer young per nest, on average, than

TABLE 1. Reproductive parameters ($\bar{x} \pm$ SE, [n]) of House Wrens nesting in suburban and rural habitats in and around the Washington, D.C.– Baltimore, Maryland metropolitan area in 2004.

	Suburban	Rural	Statistic	*P*-value
Clutch initiation[a]	115.1 ± 1.4 [15]	115.7 ± 1.2 [15]	$t_{28} = 0.29$	0.78
Clutch size[b]	6.2 ± 0.1 [33]	6.4 ± 0.1 [43]	$F_{1,69} = 0.70$	0.40
Nests with ≥ 1 fledgling (%)	88 [33]	60 [43]	$\chi^2 = 11.7$	<0.001
Fledglings/nest (all nests)	5.2 ± 0.4 [33]	3.4 ± 0.4 [43]	$Z = 2.76$	0.006
Fledglings/nest (successful nests)[b]	6.0 ± 1.4 [29]	5.7 ± 1.4 [26]	$F_{1,52} = 2.27$	0.13
Eggs producing fledglings (%)	93.0 ± 2 [29]	92.0 ± 2 [26]	$Z = -0.01$	0.99
Nestling body mass (g)[c]	10.05 ± 0.10 [29]	10.41 ± 0.11 [26]	$t_{53} = -2.45$	0.02
Nestling wing chord (mm)[c]	30.23 ± 0.29 [29]	31.34 ± 0.32 [26]	$t_{53} = -2.59$	0.01
Nestling tarsus length (mm)[c]	16.68 ± 0.05 [29]	16.79 ± 0.08 [26]	$t_{53} = -1.19$	0.24

[a] Mean Julian date for the first 15 nests with eggs in each habitat type.
[b] Least-squares means adjusted for effect of laying date (clutch size declines through the season).
[c] Taken on Day 11 of the nestling cycle.

suburban nests. Successful rural nests did not produce fewer fledglings than suburban nests after adjusting for seasonal effects on fledgling production. The mean number of fledglings per egg laid was also nearly identical for successful rural and suburban nests.

The mean mass of nestlings on NSD 11 was greater in rural nests than in suburban nests ($P < 0.02$). The difference in nestling mass was significant even after controlling for brood size which were, on average, smaller in rural nests ($F_{1,52} = 4.67$, $P < 0.04$). Similarly, nestlings had longer wing chords, on average, on NSD 11 in rural compared to suburban nests, even after controlling for brood size ($F_{1,52} = 5.97$, $P < 0.02$). Tarsus length of nestlings in rural and suburban nests did not differ.

House Wren pairs early in the nestling stage delivered prey at a greater ($P < 0.01$) rate at suburban nests than at nests in rural areas (Table 2). In contrast, we found no difference in the rate at which parents provisioned older nestlings in suburban and rural habitats. Females at rural nests spent more time brooding nestlings than females at suburban nests ($P < 0.02$; Table 2). Brooding time declined as provisioning rates increased in both habitats ($r = -0.56$, $n = 14$, $P = 0.03$).

DISCUSSION

Reproductive success of House Wrens nesting in rural and suburban habitats varied with lower fledging success in rural habitats because of greater rates of nest predation. Our results, however, were mixed. Nestlings reared in suburban areas weighed significantly less and had shorter wings compared to nestlings reared in rural areas. In an Illinois population of House Wrens, a nestling's probability of being recruited into the breeding population was positively associated with its body mass late in the nestling stage (C. F. Thompson, unpubl. data). Similar results have been reported for several species (Newton 1998).

Our result that nests in rural areas were depredated at significantly higher rates compared to nests in suburban areas was striking given that far more rural than suburban nest boxes had predator-deterrent devices (69 vs. 3% of nest boxes, respectively). Rural nests may have been depredated significantly more often because most nest boxes were on the edge of large forest fragments facing more open land-

TABLE 2. Parental behavior ($\bar{x} \pm$ SE, [n]) of House Wrens nesting in suburban and rural habitats in the Washington, D.C.–Baltimore, Maryland metropolitan area in 2004.

	Suburban	Rural	Statistic	*P*-value
Feeding rate, early[a]	3.2 ± 0.3 [9]	2.0 ± 0.2 [7]	$t_{14} = -3.31$	<0.01
Feeding rate, late[b]	4.0 ± 0.57 [10]	3.40 ± 0.6 [9]	$t_{17} = -0.79$	0.44
Minutes brooding/hr	29.0 ± 4 [8]	43.0 ± 6 [6]	$t_{12} = 2.81$	<0.02

[a] Provisionings/nestling/hr, 1–4 days post-hatching.
[b] Provisionings/nestling/hr, 9–13 days post-hatching.

scapes. Edge habitats are known to have higher numbers of predators (e.g., Patten and Bolger 2003). Most rural nest boxes were older and had been in place longer than the suburban nest boxes, giving predators the chance to learn nest locations and how to elude predator deterrent devices.

Differences in nestling body mass (Table 1) between habitats may be caused by differences in prey quantity or quality. We have no data to address this hypothesis directly and are unaware of existing data directly relevant to birds. Parents in suburban habitats appeared to deliver as many or more prey to nests compared to parents in rural habitats and yet produced lighter, smaller offspring; this suggests that prey quality may be lower in suburban areas. Consistent with this observation are the findings of Ishitani et al. (2003) who reported that insects in suburban habitats tend to be smaller than species in more natural habitats. Females in suburban habitats also spent less time brooding nestlings during our watches. We did not observe any human disturbance while watching nests in both habitats. Nestlings in suburban areas may grow more slowly because lower body temperatures cause them to process food less efficiently and invest more energy in thermoregulation at the expense of growth (Johnson and Kermott 1993, Dawson et al. 2005).

Highly disturbed environments, such as residential suburban habitats, may represent an ecological trap for some species. Leston and Rodewald (2006) failed to find any differences in reproductive success or apparent survival of Northern Cardinals breeding in forest patches within urban versus rural landscapes. Our finding that House Wrens in suburban habitats produce lighter, smaller offspring suggests these habitats may act as ecological traps. However, counter to this suggestion is the finding that suburban nests also experienced significantly lower rates of nest predation. Further work is needed to learn whether this result is an artifact of our use of nest boxes. House Wrens are common in suburban habitats which suggest sufficient young are produced in these habitats to sustain populations. Alternatively, suburban habitats may be sinks and populations rely on dispersal of individuals from other locations to maintain current densities. Research quantifying factors directly associated with habitat quality (e.g., prey availability and nest predation rates), measures of annual survival, and habitat selection in this system should provide insight into the extent urban and suburban areas act as population sinks and ecological traps for House Wrens and other native song birds.

ACKNOWLEDGMENTS

We thank the Neighborhood Nestwatch participants for permission to work on their property, J. Smith, R. J. Peters, and K. E. Roux for help in the field, and R. S. Ebersole for valuable comments on the manuscript and moral support. We also thank the Mills Corporation for financial support.

LITERATURE CITED

Beale, C. M. and P. Monaghan. 2004. Human disturbance: people as predation free predators? Journal of Applied Ecology 41:335–343.

Cam, E., J. D. Nichols, J. R. Sauer, J. E. Hines, and C. H. Flather. 2000. Relative species richness and community completeness: birds and urbanization in the Mid-Atlantic States. Ecological Applications 10:1196–1210.

Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation 78:69–96.

Czapka, S. J. and L. S. Johnson. 2000. Consequences of mate sharing for first-mated females in a polygynous songbird, the House Wren. Wilson Bulletin 112:72–81.

Dawson, R. D., C. C. Lawrie, and E. L. O'Brien. 2005. The importance of microclimate variation in determining size, growth and survival of avian

offspring: experimental evidence from a cavity nesting passerine. Oecologia 144:499–507.

Donnelly, R. 2002. Design of habitat reserves and settlement for bird conservation in the Seattle metropolitan area. Dissertation. University of Washington, Seattle, USA.

Donnelly, R. and J. M. Marzluff. 2004. Importance of reserve size and landscape context to urban bird conservation. Conservation Biology 18:733–745.

Donovan, T. M. and F. R. Thompson. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecological Applications 11:871–882.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064–2075.

Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.

Giese, M. 1996. Effects of human activity on Adelie Penguin *Pygoscelis adeliae* breeding success. Biological Conservation 75:157–164.

Goldstein, E. L., M. Gross, and R. M. DeGraff. 1986. Breeding birds and vegetation: a quantitative assessment. Urban Ecology 9:377–385.

Hennings, L. A. and W. D. Edge. 2003. Riparian bird community structure in Portland, Oregon: habitat, urbanization, and spatial scale patterns. Condor 105:288–302.

Ishitani, M., D. J. Kotze, and J. Niemela. 2003. Changes in carabid beetle assemblages across an urban-rural gradient in Japan. Ecography 26:481–489.

Johnson, L. S. 1998. The House Wren (*Troglodytes aedon*). The birds of North America. Number 380.

Johnson, L. S. and L. H. Kermott. 1993. Why is reduced male parental assistance detrimental to the reproductive success of secondary female House Wren? Animal Behaviour 46:1111–1120.

Kokko, H. and W. J. Sutherland. 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research 3:537–551.

Leston, L. and A. D. Rodewald. 2006. Are urban forests ecological traps for understory birds? An examination using Northern Cardinals. Biological Conservation 131:566–574.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19–47 *in* Avian ecology and conservation in an urbanizing world (J. M. Marzluff, R. Bowman, and R. Donnelly, Editors). Kluwer Academic, Norwell, Massachusetts, USA.

Mills, G. S., J. B. Dunning Jr., and J. M. Bates. 1991. The relationship between breeding bird density and vegetation volume. Wilson Bulletin 103: 468–479.

Misenhelter, M. D. and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. Ecology 81:2892–2901.

Morrison, B. L. and L. S. Johnson. 2002. Feeding of House Wren nestlings afflicted by hematophagous ectoparasites: a test of the parental compensation hypothesis. Condor 104:183–187.

Negative Population Growth. 2005. Maryland's population in 2050: is smart growth enough? http://www.npg.org/polls091200/md (accessed 22 June 2005).

Newton, I. 1998. Population limitation in birds. Academic Press. London, United Kingdom.

Obendorf, S. K., A. T. Lemley, A. Hedge, A. A. Kline, K. Tan, and T. Dokuchayeva. 2006. Distribution of pesticide residues within homes in central NY State. Archives of Environmental Contamination and Toxicology 50:31–44.

Patten, M. A. and D. T. Bolger. 2003. Variation in top-down control of avian reproductive success across a fragmentation gradient. Oikos 101:479–488.

Pavlik, J. and S. Pavlik. 2000. Some relationships between human impact, vegetation, and birds in urban environments. Ekologia-Bratislava 19:392–408.

Purcell, K. L. and J. Verner. 1998. Density and reproductive success of California Towhees. Conservation Biology 12:442–450.

Resumeš, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics? Oikos 91:579–582.

Robinson, S. K., F. R. Thompson III, and T. M. Donovan. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987–1990.

SAS Institute. 1999. SAS/STAT user's guide. Release 8.1. SAS Institute Inc., Cary, North Carolina, USA.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474–480.

Thorington, K. K. and R. Bowman. 2003. Predation rate on artificial nests increases with human housing density in suburban habitats. Ecography 26: 188–196.

Weldon, A. J. and N. M. Haddad. 2005. The effects of patch shape on Indigo Buntings: evidence for an ecological trap. Ecology 86:1422–1431.

The Wilson Journal of Ornithology 120(1):105–110, 2008

HABITAT SELECTION AND REPRODUCTIVE SUCCESS OF CERULEAN WARBLERS IN INDIANA

KIRK L. ROTH[1] AND KAMAL ISLAM[1,2]

ABSTRACT.—We studied the breeding habitat of Cerulean Warblers (*Dendroica cerulea*) in southern Indiana in the Ohio River Valley in 2002–2003 to identify similarities and differences in habitat characteristics compared to breeding habitats reported for this species in other geographical regions. Ten 259-ha study plots were surveyed for Cerulean Warblers and territories were mapped using locations of perched, singing males. We measured slope and vegetation characteristics including canopy height and cover, ground cover, number of shrubs and shrub species, number of trees, DBH, and number of snags at Cerulean Warbler territories and non-use sites. Habitat characteristics associated with Cerulean Warbler territories compared to non-use sites were higher canopy height (28 m) and cover (84%), larger trees (>38 cm DBH), higher slope (11°), fewer number of trees (30), and fewer trees between 3 and 23 cm DBH. Calculated Mayfield estimate of nest productivity (0.165) was lower compared to Mississippi Alluvial Valley sites (0.242). *Received 23 December 2006. Accepted 17 July 2007.*

The Cerulean Warbler (*Dendroica cerulea*) is one of the fastest-declining neotropical migrants in North America (Robbins et al. 1992) and populations declined at an average annual rate of 3.04% between 1966 and 2000 (Robbins et al. 1992, Link and Sauer 2002). The breeding range of the Cerulean Warbler includes most of the Midwest, from the Mississippi Alluvial Valley north into southern Ontario, Canada (Hamel 1992) and much of the northeastern United States. Large population losses have been reported in the Midwest, which represents the center of the species' distribution (Dunn and Garrett 1997). Despite an increase in forest cover during the last 50 years in the northeastern United States, loss of suitable breeding habitat likely is a major cause of Cerulean Warbler population declines. Fragmentation of suitable forest habitat is prominent in the agricultural areas of the Midwest and Mississippi Alluvial Valley within the range of this species (Robbins et al. 1992).

The breeding habitat of Cerulean Warbler has been described as deciduous forest with large, tall trees (Lynch 1981, Hamel 2000a, Jones and Robertson 2001). However, differences in habitat characteristics have been noted across the range of the species (Hamel 2000a) and Hamel (2000b) suggested that Cerulean Warblers do not exhibit a rangewide nesting tree preference. Specific tree preferences may occur in different localities within the breeding range (Oliarnyk and Robertson 1996; Dunn and Garrett 1997; Hamel 2000a, b; Barg et al. 2006). Other aspects of Cerulean Warbler breeding habitat, such as nest height (Hamel 2000a) and forest tract size (Peterjohn and Rice 1991, Robbins et al. 1992) also vary rangewide. Differences in specific breeding habitat characteristics among geographical regions suggest that habitats suitable for Cerulean Warblers in one area may be unsuitable for populations in other locations. Variability in habitat preferences, which could reflect tree species availability or specific site-dependent parameters, has implications for site-specific habitat management to benefit Cerulean Warbler populations.

Identification of preferred vegetative structure is considered a high research priority for conservation of Cerulean Warblers (Hamel 2000a). Studies of the breeding biology of Cerulean Warblers are needed for many geographical locations throughout its distribution (Hamel 2000a, Hamel et al. 2004). Research focusing on breeding biology of Cerulean Warblers is difficult because the species typically nests in the canopy 9–15 m above ground level (Hamel 2000a, Jones and Robertson 2001). Investigation of nest productivity requires intensive study and has been rarely undertaken (Oliarnyk and Robertson 1996, Hamel 2000a). The only published studies on Cerulean Warbler nest characteristics and productivity are from research sites in Ontario, Canada (Oliarnyk and Robertson 1996, Jones and Robertson 2001, Hamel et al. 2004, Jones et al. 2004), and Michigan (Rogers 2006).

[1] Department of Biology, Ball State University, Muncie, IN 47306, USA.

[2] Corresponding author; e-mail: kislam@bsu.edu

Our objectives were to: (1) identify breeding habitat characteristics of Cerulean Warbler territories in southern Indiana, (2) compare characteristics of Cerulean Warbler territories with randomly selected non-use sites, (3) compute nest survival, and (4) ascertain if there were any demonstrated site-specific breeding habitat preferences.

METHODS

Study Area.—We conducted our study in the 20,234-ha Big Oaks National Wildlife Refuge (39° 03′ N, 85° 25′ W) in Jefferson, Jennings, and Ripley counties, Indiana. Ten 259-ha (1 mi^2) study plots with deciduous forest were selected in the northern third of the refuge based on the presence of Cerulean Warblers. The forest in the study plots was dominated by oak (*Quercus* spp.), hickory (*Carya* spp.), and maple (*Acer* spp.). Each (259-ha) plot was grid-marked at 200-m intervals resulting in 49 interval points to facilitate mapping of territories and vegetation sampling.

Bird Surveys.—We conducted surveys of male Cerulean Warblers within the study plots from early May through late June in 2002 and 2003. Each plot was surveyed once during each breeding season. We used a 100-m fixed-radius point count for 3-min at each grid interval (Hutto et al. 1986). Cerulean Warblers in our study area prominently and strongly sang from selected song perches and playback was often unnecessary. We attempted to elicit a response using playbacks of Cerulean Warbler songs to simulate territory occupancy if Cerulean Warblers were not detected (Falls 1981). We played the recording for 2 min at a broadcast covering an area with a 100-m radius using a Sony WM-FX281 walkman with a Radio Shack Model 540-1441 speaker. Bird surveys were conducted during peak activity times between 0530 and 1000 hrs EST and not during rainy or windy weather. We mapped Cerulean Warbler territories from mid-May through early July. Territories were defined by locations of perched, singing males and were demarcated using locations of observations and bird responses to playbacks. Playbacks of another territorial male outside the territory boundary have been demonstrated to cause male songbirds to sing at the edge of their own territories (Falls 1981). All birds drawn by playback moved distances ≤50 m (K. L. Roth, pers. obs.). No territories in the study plots overlapped or were adjacent to one another. A territory was considered to be completely mapped when the bird indicated no new song perches, even in response to playbacks. Complete territory mapping involved a time period of 1–4 days. Universal Transverse Mercator (UTM) coordinates were recorded along territorial boundaries using a Global Positioning System (GPS) unit with NAD 83 datum and later mapped using the ArcInfo computer program (ESRI 1996).

Vegetation Sampling.—We sampled vegetation within each of the 71 territories detected and at an equal number of randomly selected sites in the study plots from early July to mid-August each year (James and Shugart 1970). The approximate center of each territory, located by pacing and halving the length and width of the territory, was used as the center of the vegetation sampling plot. Random sites were selected by applying a random numbers table to the grid setup of the study plots. One random site was selected for each mapped territory. All vegetation sampling plots comprised a 11.3-m radius circle (0.04 ha). We sampled canopy cover and ground cover at 2-m intervals in each cardinal direction within the plot, using a densiometer, which resulted in a total of five readings in each direction. Slope was measured using a clinometer at the edges of the plot in each cardinal direction. Habitat characteristics measured within the 11.3-m radius plots included diameter at breast height (DBH) for trees and snags with a DBH >5 cm, mean tree height, percent canopy cover, and density of trees, snags, and shrubs. We measured DBH for woody species <5 cm (defined as shrubs) within a 5.0-m radius of the center of the plot. We estimated canopy height using a clinometer in each quarter of the plot. Trees and shrubs were separated into five size classes to categorize tree, snag, and shrub densities: (3–7.9, 8–14.9, 15–22.9, 23–37.9, and >38 cm).

We measured vertical stratification using methods modified from Hubbel and Foster (1986). Vertical stratification was estimated from 22.8 m toward the opposite border at plot borders in each cardinal direction. Vertical stratification was recorded using cover estimates at five height intervals (<2, <5, <10,

<20, and >20 m) on a stratification pole. We scored vertical stratification at each height interval on a scale of 1 to 6: 1 (1–7% cover), 2 (8–25% cover), 3 (26–50% cover), 4 (51–75% cover), 5 (76–93% cover), or 6 (94–100% cover).

Vegetation Analysis.—Differences between vegetation components at territorial and randomly selected non-use sites were analyzed with *t*-tests for equality of means using SPSS (SPSS Inc. 2002). Logistic regressions were used for variable comparisons between random and territorial sites for: number of shrub species, number of shrubs, vertical stratification classes, overall mean DBH, number of trees including snags, all DBH classes, canopy height, canopy cover, ground cover, and slope. Canopy cover, ground cover, canopy height, and slope readings were combined for analysis in each plot. Vegetative characteristics are reported as means ± standard deviation.

Nest Site Characterization and Nest Survival.—We located Cerulean Warbler nests using behavioral cues from adults. Vegetative parameters of nest trees were sampled using the Bbird field protocol (Martin et al. 1997). We measured DBH, horizontal distance to the foliage edge of the nest tree, and horizontal distance to the nest tree trunk for each nest tree. We recorded nest tree species and vegetative species that provided concealment above the nest. Nest height was estimated using a clinometer. Tree species and DBH of Cerulean Warbler song perch trees from territory mapping were used as comparisons for nest trees (Barg et al. 2006). Nest and perch tree differences were analyzed using *t*-tests of equality of means using SPSS (SPSS Inc. 2002). Differences between nest tree species and expected tree species based upon occurrence in the territory were considered, but nest tree sample size was too small for an associative test. Nest tree vegetative characteristics are reported as means ± standard deviation. Each nest was monitored from the ground using binoculars and spotting scopes. We observed and recorded the number of days the nest was in the building, incubation, and brooding stages using parental activity as an indicator. Nesting stages were designated conservatively given the difficulty of observing Cerulean Warbler nests. Thus, a bird was required to show definitive behavior to indicate the nesting stage. Timing of these stages was confirmed using average nest data (Hamel 2000a). Due to frequent nest observation, no nests had uncertain fail dates. These data were used for Mayfield estimates of nest productivity (Mayfield 1975).

RESULTS

Territorial Characteristics.—There were differences ($P < 0.05$) in five characteristics (canopy cover and height, slope, number of trees, and DBH) between Cerulean Warbler territories ($n = 71$) and random ($n = 71$) sites (Table 1). Overall canopy height and cover were significantly greater in territories than at random sites. Cerulean Warbler territories had significantly higher slope but fewer number of trees than random sites (Table 1). Number of shrubs, number of shrub species, number of snags, and vertical stratification at all height intervals did not differ between territories and random sites.

The number of trees for three of five DBH classes (3–7.9, 8–14.9, and 15–22.9 cm) was significantly greater in random sites than territories but there were significantly more trees >38 cm DBH present in territories than random sites (Table 1). The number of trees between 23 and 37.9 cm DBH did not differ between territories and random sites.

Important predictive components, based on logistic regression analyses, included canopy height ($\beta = 0.089$, SE = 0.030, $P = 0.003$), number of trees ($\beta = -0.025$, SE = 0.012, $P = 0.036$), and slope ($\beta = 0.093$, SE = 0.039, $P = 0.016$) with a 67.2% predictive value for Cerulean Warbler territories. The probability that a site is used as a Cerulean Warbler territory increased with increasing canopy height and slope, and decreased with increasing number of trees.

Nest Tree Characteristics and Nest Survival.—Tulip trees (*Liriodendron tulipifera*) were widely available, but use as nest trees by Cerulean Warblers was low. Fifty-three percent of nest trees were either black walnut (*Juglans nigra*) or white oak (*Quercus alba*). Fourteen nest trees included 9 black walnuts, 2 sweetgums (*Liquidambar styraciflua*), 2 black locusts (*Robinia pseudoacacia*), and 1 eastern sycamore (*Platanus occidentalis*). Thirty-three percent of nests were concealed by Virginia creeper (*Parthenocissus quinquefolia*).

TABLE 1. Vegetative characteristics at Cerulean Warbler territories and random sites at Big Oaks National Wildlife Refuge, Indiana during 2002 and 2003. Canopy and ground cover measurements were on a scale of 0–5, with 5 being complete cover. Stratification values were coded on a scale of 1–6 following Hubbel and Foster (1986).

	Territory			Random			Results of *t*-test		
Vegetation parameter	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	*t*	df	*P*
Canopy cover	4.19	0.59	58	3.91	0.78	58	−2.181	114	0.031
Ground cover	2.77	1.11	58	2.97	1.14	58	0.972	114	0.33
Slope (degrees)	10.87	6.9	58	7.13	5.31	58	−3.275	114	0.001
Canopy height (m)	28.19	6.49	56	24.07	7.35	58	−3.18	112	0.002
Number shrubs	1.92	2.51	56	1.61	1.54	54	−1.135	235	0.25
Number shrub species	2.69	1.7	39	2.51	1.79	41	−0.46	78	0.64
Number trees	29.7	13.13	56	42.9	29.27	54	3.047	72.9	0.003
DBH (cm)	22.8	2.98	56	20.7	5.19	54	−2.595	83.6	0.011
Number snags	5.05	4.98	56	7.01	7.51	54	1.611	91.6	0.11
Number trees									
3–7.9 DBH	11.8	10.02	56	17.6	18.66	54	2.055	80.5	0.043
8–14.9 DBH	5.8	5.78	56	10.6	10.59	54	3.49	73.7	0.001
15–22.9 DBH	3.6	3.61	56	6.6	6.61	54	3.683	81	<0.001
23–37.9 DBH	4.4	4.37	56	4.9	4.91	54	0.798	105.2	0.42
>38 DBH	3.6	3.59	56	2.6	2.56	54	−2.482	96	0.015
Vertical cover									
0–2.5 m	3.25	1.52	58	3.34	1.3	57	0.316	113	0.75
2.5–5 m	2.88	1.24	58	3.08	1.24	57	0.902	113	0.36
5–10 m	3.29	1.07	58	3.3	1.24	57	0.064	113	0.94
10–15 m	3.83	1.04	58	3.7	1.23	57	0.614	113	0.54
>15 m	3.95	1.02	58	4.06	1.16	57	−0.553	113	0.58

All nests not concealed by Virginia creeper were concealed by the foliage of the nest tree.

DBH was greater for nest trees ($\bar{x}$ = 50.4 ± 25.8 cm) compared to trees at random sites, trees in territories ($\bar{x}$ = 22.81), and song perch trees. Nest tree height was variable and averaged 18.38 ± 5.08 m (n = 43). Nest distance from trunk averaged 4.8 ± 2.4 m. Nest distance from foliage edge averaged 2.9 ± 1.5 m.

Forty of 43 nests located contained eggs or nestlings. Thirty-three of 40 active nests failed and 7 fledged young (Table 2). Mayfield estimates of nest productivity gave a seasonal survival probability of 0.165 for both years. The Mayfield estimate was higher during 2002 (0.335) than during 2003 (0.0899) (Table 2).

TABLE 2. Number of Cerulean Warbler territories surveyed and nest productivity data, including Mayfield estimates (Mayfield 1975) at Big Oaks National Wildlife Refuge, Indiana during 2002 and 2003.

Parameter	2002	2003	Totals
Territories	42	29	71
Fledged nests	4	3	7
Failed nests	10	23	33
Mayfield estimate	0.335	0.0899	0.165

DISCUSSION

Important characteristics associated with Cerulean Warbler territories were tall tree canopy, higher percent of canopy cover, higher slope, more trees >38 cm DBH, fewer number of trees, and fewer trees between 3 and 22.9 cm DBH than random sites. Factors that did not appear to be important in Cerulean Warbler territory selection included vertical stratification, number of snags, shrub cover, and ground cover.

The vegetative characteristics of Cerulean Warbler territories in our study area were similar to those reported in other studies of Cerulean Warblers (Lynch 1981, Kahl et al. 1985, Jones and Robertson 2001, Weakland and Wood 2005). Territorial canopy cover in our study averaged 83.7%, similar to the 85% in Missouri (Kahl et al. 1985). There was a

significant difference in tree density between territorial and random sites in our study but not in Ontario (Jones and Robertson 2001). Our study supports others (Robbins et al. 1992, Hamel 2000a, Jones and Robertson 2001, Barg et al. 2006, Jones and Islam 2006) that Cerulean Warblers select large trees for nesting and perching. Oliarnyk and Robertson (1996) reported that large nest tree size was an important factor for nest success. DBH was larger for nest trees compared to territorial site and song perch trees in our study, indicating that Cerulean Warblers select for the largest trees within their territories for nest sites. Some form of nest concealment was found at all nests of Cerulean Warblers at Big Oaks National Wildlife Refuge. Live Virginia creeper was an important component for nest concealment, overhanging a third of all nests located. No Cerulean Warbler nest was concealed by any other vine, despite an abundance of grapes (*Vitis* sp.) and poison ivy (*Toxicodendron radicans*) (K. L. Roth, pers. obs.). The denser foliage of Virginia creeper may present a more attractive cover for Cerulean Warblers at Big Oaks National Wildlife Refuge, which otherwise build nests only under extensive cover provided by the leaves of the nest tree.

Cerulean Warblers appear to be consistent in selecting the largest trees in territories, but there is no definitive optimal tree size. The average nest height of 18.4 m in our study is higher than the average height of 11.8 m for nests in Ontario (Oliarnyk and Robertson 1996) and the 11.4 m (n = 80) rangewide reported by Hamel (2000b). However, nest height at sites reported in Michigan was slightly higher (19–20 m; Rogers 2006). Thus, Cerulean Warblers select the largest trees for territorial and nesting activities. Most territories in our study were in topographically diverse areas and particularly near drainages. This is evident from higher slopes associated with Cerulean Warbler territories compared to random sites. However, a small number of territories were also noted in several floodplain areas of our study area.

We recorded low nest success with our Mayfield estimate of 0.165 compared with a 0.242 success for 66 nests at three Mississippi Alluvial Valley sites (Hamel 2000a). Our Mayfield estimate assumed that all eggs present at hatch time will produce living young and actual survival of young may be lower than estimated.

We did not observe any brood parasitism. We suspected predation was a major cause of nest loss. Potential nest predators including American Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), and rat snakes (*Elaphe obsoleta*) were commonly found in Cerulean Warbler nesting areas. We observed one nest being depredated by an American Crow and another failed nest had remains of a torn wing with pinfeathers directly underneath (K. L. Roth, pers. obs.). Another possible cause of nest failure is weather-related events (Jones et al. 2001). Southern Indiana experienced two unseasonably cold periods of below 5° C temperatures in late May–early June 2003. Four of 14 (29%) and 4 of 7 (57%) active nests failed during the first and second cold spells, respectively.

Some habitat characteristics appear to be common to Cerulean Warblers throughout the breeding range of the species. However, territorial characteristics may be unique to a specific population within a region. Tree size and forest moisture regime may not be useful as rangewide defining characteristics of Cerulean Warbler habitat. These factors, combined with the variability in size of forest tract selected by this species (Peterjohn and Rice 1991, Robbins et al. 1992, Hamel 2000a) make habitat characterization difficult. Our data may only be useful for Cerulean Warbler habitat management in the Ohio River Valley. A single rangewide management approach may not be an appropriate strategy for this species. We recommend greater emphasis on formulating and implementing site-specific management recommendations to conserve important habitat features. These studies should be undertaken to identify Cerulean Warbler habitat in all major areas of this species' breeding range including sites within Appalachia, Wisconsin, and the Ozark Mountains. Cerulean Warblers have an affinity for the habitat in our study area, but further research is required to identify critical habitat characteristics associated with nest success/productivity. Research attention should be given to habitat issues such as canopy gaps, horizontal vegetative complexity, and canopy foliage configuration (Hamel 2000a),

ACKNOWLEDGMENTS

This research was supported, in part, by the U.S. Fish and Wildlife Service, Garden Club of America, Indiana Academy of Science, Sigma Xi, and Ball State University Office of Academic Research and Sponsored Programs. We thank Joseph Robb for permission to work at Big Oaks National Wildlife Refuge and his staff for field support. We thank refuge staff, Teresa Vanosdol, Jason Lewis, and Laura Lake, and our field crew, K. C. Jones, Joseph Allen, Holly Adams, Dustin Varble, Elizabeth Shaefer, Kendra Darnell, Kate Haddan, Amy Saylor, Eric Suttles, and C. R. Ward for assistance in data collection. We are grateful to Jason Jones and Randy Dettmers for contributing their expertise and time in the field. Analytical assistance was provided by James Jones. This manuscript benefited from the critical comments and suggestions of two anonymous reviewers and the editor.

LITERATURE CITED

Barg, J. J., D. M. Aiama, J. Jones, and R. J. Robertson. 2006. Within-territory habitat use and microhabitat selection by male Cerulean Warblers (*Dendroica cerulea*). Auk 123:795–806.

Dunn, J. L. and K. L. Garrett. 1997. A field guide to warblers of North America. Houghton-Mifflin, Boston, Massachusetts, USA.

ESRI. 1996. ArcView GIS. Environmental Systems Research Institute Inc., Redlands, California, USA.

Falls, J. B. 1981. Mapping territories with playback: an accurate census method for songbirds. Studies in Avian Biology 6:86–91.

Hamel, P. B. 1992. Cerulean warbler, *Dendroica cerulea*. Pages 385–400 *in* Migratory nongame birds of management concern in the Northeast (K. J. Schneider and D. M. Pence, Editors). USDI, Fish and Wildlife Service, Newton Corner, Massachusetts, USA.

Hamel, P. B. 2000a. Cerulean Warbler (*Dendroica cerulea*). The birds of North America. Number 511.

Hamel, P. B. 2000b. Cerulean Warbler status assessment. USDI, Fish and Wildlife Service, Minneapolis, Minnesota, USA.

Hamel, P. B., D. K. Dawson, and P. D. Keyser. 2004. How we can learn more about the Cerulean Warbler (*Dendroica cerulea*). Auk 121:7–14.

Hubbel, S. P. and R. B. Foster. 1986. Canopy gaps and the dynamics of a neotropical forest. Pages 77–95 *in* Plant ecology (M. J. Crawley, Editor). Blackwell Scientific Publications, Oxford, United Kingdom.

Hutto, R. L., S. M. Pletschet, and T. P. Hendricks. 1986. A fixed-radius point-count method for nonbreeding and breeding season use. Auk 103:593–602.

James, F. C. and H. H. Shugart Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Jones, J. and R. J. Robertson. 2001. Territory and nest-site selection of Cerulean Warblers in eastern Ontario. Auk 118:727–735.

Jones, J., R. D. DeBruyn, J. J. Barg, and R. J. Robertson. 2001. Assessing the effects of natural disturbance on a neotropical migrant songbird. Ecology 82:2628–2635.

Jones, J., J. J. Barg, T. S. Sillett, M. L. Veit, and R. J. Robertson. 2004. Minimum estimates of survival and population growth for Cerulean Warblers (*Dendroica cerulea*) breeding in Ontario, Canada. Auk 121:15–22.

Jones, K. and K. Islam. 2006. Selection of song perches by Cerulean Warblers. Proceedings of the Indiana Academy of Science 115:37–43.

Kahl, R. B., T. S. Baskett, J. A. Ellis, and J. N. Burroughs. 1985. Characteristics of summer habitats of selected nongame birds in Missouri. Agriculture Experiment Station Research Bulletin 1056. University of Missouri, Columbia, USA.

Link, W. A. and J. R. Sauer. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. Ecology 83:2832–2840.

Lynch, J. M. 1981. Status of the Cerulean Warbler in the Roanoke River Basin of North Carolina. Chat 45:29–35.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Oliarnyk, C. J. and R. J. Robertson. 1996. Breeding behavior and reproductive success of Cerulean Warblers in southeastern Ontario. Wilson Bulletin 108:673–684.

Peterjohn, B. G. and D. L. Rice. 1991. The Ohio breeding bird atlas. Division of Natural Areas and Preserves, Ohio Department of Natural Resources, Columbus, USA.

Robbins, C. S., J. W. Fitzpatrick, and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. Pages 549–562 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan and D. W. Johnston, Editors). Smithsonian Institute Press, Washington D.C., USA.

Rogers, C. M. 2006. Nesting success and breeding biology of Cerulean Warblers in Michigan. Wilson Journal of Ornithology 118:145–151.

SPSS Inc. 2002. SPSS. Version 11.5. Chicago, Illinois, USA.

Weakland, C. A. and P. B. Wood. 2005. Cerulean Warbler (*Dendroica cerulea*) microhabitat and landscape-level habitat characteristics in southern West Virginia. Auk 122:497–508.

The Wilson Journal of Ornithology 120(1):111–119, 2008

NESTING BIOLOGY OF GRASSLAND BIRDS AT FORT CAMPBELL, KENTUCKY AND TENNESSEE

JAMES J. GIOCOMO,[1,3] E. DANIEL MOSS,[2] DAVID A. BUEHLER,[1] AND WILLIAM G. MINSER[1]

ABSTRACT.—Grassland birds have experienced greater population declines than any other group of birds monitored by the North American Breeding Bird Survey. Our goal was to compare demographic rates among years within species and among species of grassland birds. Eight-hundred and eleven nests of Henslow's Sparrows (*Ammodramus henslowii*), Grasshopper Sparrows (*A. savannarum*), Field Sparrows (*Spizella pusilla*), Dickcissels (*Spiza americana*), and Eastern Meadowlarks (*Sturnella magna*) were monitored between 1999 and 2003. Mayfield nest success including the egg-laying stage, as well as the incubation and nestling periods, was 20, 34, 15, 20, and 18%, respectively. Most nest failures were attributed to predation. Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) was infrequent (<2% of all nests parasitized). Clutch size decreased during the nesting season for Dickcissels, Grasshopper Sparrows, and Field Sparrows. Nesting phenology suggests the possibility of multiple-brooding for all five species in this study. *Received 21 February 2006. Accepted 14 April 2007.*

Grassland bird population declines have been attributed to the dramatic decrease of native grasslands during the 20th century because of clearing of non-forested land for agriculture or development, and discontinued use of prescribed fire (Askins 1993, Herkert et al. 1996, Peterjohn and Sauer 1999). Military lands in the eastern United States are an exception to the trend in loss of native grasslands. Some installations have maintained large areas of grasslands through use of prescribed burning and mowing to facilitate military training. For example, Fort Campbell Military Reservation in Kentucky and Tennessee, a 42,000-ha U.S. Army Base, has ~10,000 ha of grassland habitat including remnant patches of native grassland (Moss 2001). Several other military installations in the eastern United States including Fort Knox, Kentucky, Fort Bragg, North Carolina, and Fort Drum, New York, also have large areas of early-successional habitats (Eberly 2002).

It is important to understand not only the distribution of grassland bird species in the eastern United States, but also their productivity. Many studies report densities and diversity of bird species, but these measures may be misleading indicators of habitat quality or breeding success (Van Horne 1983, Vickery et al. 1992). Few studies have collected detailed demographic information needed to understand productivity (i.e., nesting success, clutch size) (Marzluff and Sallabanks 1998). Many grassland bird nests are difficult to find and monitor, and relatively few studies have attempted to monitor more than one to two species for more than a few years (Winter 1998). Managers of military installations need demographic information to understand if and how their management actions and military training may impact bird populations.

We monitored Henslow's Sparrow (*Ammodramus henslowii*), Grasshopper Sparrow (*A. savannarum*), Field Sparrow (*Spizella pusilla*), Dickcissel (*Spiza americana*) and Eastern Meadowlark (*Sturnella magna*) nests at Fort Campbell from 1999 through 2003. Our objectives were to obtain annual, species-specific demographic information including nest success, clutch size, young produced per successful nest, causes for nest failure, nest parasitism rates, timing of nest initiation, and seasonal clutch size variation, and to compare these demographic rates among years within species and among species.

METHODS

Study Area.—The study was conducted on Fort Campbell on the Kentucky-Tennessee

[1] Department of Forestry, Wildlife and Fisheries, University of Tennessee, 274 Ellington PSB, Knoxville, TN 37996, USA.

[2] Directorate of Public Works, IMSE-CAM-PWE, 865 16th Street, Fort Campbell, KY 42223, USA.

[3] Corresponding author; e-mail: jgiocomo@utk.edu

border. Fort Campbell contains some of the largest remaining blocks of native prairie "barrens" east of the Mississippi River. Barrens are grass-dominated, treeless areas occurring on the hilly, karst topography of west-central Kentucky and northwestern Tennessee (Chester et al. 1997). Historically, these grasslands were maintained primarily through burning by native Americans (Delcourt et al. 1993). Many grasslands on Fort Campbell contain at least some native warm-season grasses including little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), and broomsedge (*Andropogon virginicus*). Approximately 60% of the area is in oak (*Quercus* sp.)-hickory (*Carya* sp.) forests with many leased agricultural fields (cool-season grasses, corn, millet, and soybeans) interspersed among the grasslands. Most of the grassland areas monitored in this study were managed mainly for military training and not specifically for hay production.

Nest Searching.—We concentrated primarily on finding an adequate sample (~20) of nests each year for our five target species including Henslow's Sparrow, Grasshopper Sparrow, Dickcissel, Eastern Meadowlark, and Field Sparrow. Fields with appropriate grassland habitat, such as dead standing clumps of grass, were systematically searched by one crew leader and four field assistants for males of target species defending territories or exhibiting nesting behavior between 1 May and 31 July, 1999–2003. Fields were selected to provide the maximum opportunity to find a representative sample of nests for the more difficult species to monitor, especially Henslow's Sparrows. Most fields on Fort Campbell are burned every 1–3 years; thus, a different set of fields was searched each year allowing us to search in areas with dead standing vegetation that is not present the first year after a field is burned. Up to 20 fields were searched each year, but most nest searching was concentrated in a few larger fields (>150 ha) that provided habitat for all five species in all years. Field sizes ranged from 4 to 600 ha. Behavioral cues, such as birds flushing close to an observer, chipping, carrying nesting material, or carrying food or fecal sacs, were used to locate nest sites.

Once nests were located, a flag was placed at least 5 m from the nest and detailed maps of the nest locations were drawn. Nests were monitored every 2–4 days to ascertain nest fate. We calculated apparent yearly nest success (successful nests/total nests), Mayfield (1961, 1975) nest success, and standard error for individual species where sample sizes were sufficient (~9 nests, Johnson 1979).

Demographic Rate Estimates.—Average clutch size was calculated using the highest number of eggs or young for nests with a stable clutch size for two consecutive visits. Successful nests were defined as any nest fledging at least one host young. Nests with no exposure time (e.g., induced fledging when the nest was found) were not included in nest success calculations. We calculated daily survival rates and the probability of nesting success for five periods: egg laying, incubation, nestling, incubation and nestling combined, and all periods. The combined probability of nesting success during the incubation and nestling stages was calculated to facilitate comparison with studies that did not explicitly include the egg laying stage.

We used mean period lengths as exponents to calculate the probability of nest success from daily survival probabilities for each species. We rounded mean clutch size to the nearest half-egg for the mean number of days during the egg laying stage for each species. Generally, one egg is laid per day for the five target species until the clutch is completed with incubation starting with laying of the last egg. We used published values for mean number of days for the incubation and nestling stage (Ehrlich et al. 1988). The number of days in the incubation and nestling stages combined, and all stages combined was the sum of the appropriate number of days in the respective component stages. Mean and standard errors for daily survival probabilities, and mean nest success were calculated by nesting period and year for each species (Johnson 1979).

Statistical Analysis.—Yearly means of young per successful nest were compared within species using one-way ANOVA. Nest initiation dates were estimated to the day laying started by back dating from the day the nest was found. Average start and end dates of nest initiation were calculated by averaging the first and last 10% of all nests combined

TABLE 1. Demographic data for Henslow's Sparrow, Grasshopper Sparrow, Dickcissel, Eastern Meadowlark, and Field Sparrow at Fort Campbell, Kentucky, 1999–2003.

	Henslow's Sparrow (n = 113)[a]	Grasshopper Sparrow (n = 131)[a]	Dickcissel (n = 204)[a]	Eastern Meadowlark (n = 87)[a]	Field Sparrow (n = 276)[a]
Successful nests	65	85	87	36	126
Unknown fate	1	0	0	1	0
Failed nests	47	46	117	50	150
Depredated	44	38	97	45	139
Abandoned	3	3	9	2	7
Abandoned-parasitized	0	0	0	0	1
Mowing for hay	0	4	4	1	2
Military activity	0	1	3	0	0
Weather	0	0	4	2	1
Apparent nest success, %	58	65	43	41	46
Clutch size average (n)	4.1(108)	4.4(131)	4.3(191)	4.6(87)	3.6(264)
Hatching success, % (n)	90.4(80)	93.2(104)	90.3(116)	94.1(53)	95.9(171)
Young fledged/nest	2.2	2.6	1.7	1.7	1.6
Young fledged/successful nest	3.9	4.1	3.9	4.0	3.6
Parasitized nests	1	0	0	0	3

[a] n = number of nests.

for each species. We used the difference between start and end dates as a measure of the minimum window of time available for each species to initiate nesting (nest initiation window). We used linear regression to examine the relationship between clutch size and nest initiation dates. We used program CONTRAST (Sauer and Hines 1989) to test for differences among daily survival rates within species, comparing different nesting intervals, and among species. The level of significance was set at $\alpha = 0.05$ and we used a Bonferroni correction to adjust our level of significance for multiple tests (Zar 1998).

RESULTS

Eight-hundred and eleven nests were monitored between 1999 and 2003; apparent nest success ranged between 41 and 65% for each species (Table 1). Most nest failures were attributed to predation. The primary predators of nests appeared to be snakes based on numerous observations of snakes in nests. Other causes of nest failures included abandonment, hay mowing and harvesting, military training activities, and Brown-headed Cowbird (*Molothrus ater*) parasitism (Henslow's Sparrow = 1, Field Sparrow = 3; Table 1). Average clutch size ranged from 3.6 for Field Sparrows to 4.6 eggs for Eastern Meadowlarks. Hatching success ranged from 90% for Dickcissels and Henslow's Sparrows to 96% for Field Sparrows (Table 1). Average young fledged per nest ranged from 1.6 to 2.6, and the average number of young per successful nest ranged from 3.6 for Field Sparrows to 4.1 for Grasshopper Sparrows (Table 1).

Eastern Meadowlarks initiated nests earliest with average nest incubation starting on 16 April. Field Sparrow nest initiation started on 25 April followed by Henslow's Sparrows (27 Apr) and Grasshopper Sparrows (1 May). Dickcissels consistently were the last species to arrive and began incubation on 10 May. The average end of the nest initiation window was between 28 June and 4 July for all five species, but active nests were found through August for all species. The length of the nest initiation window was longest for Eastern Meadowlarks (75 days), intermediate for Henslow's Sparrows (63 days), Grasshopper Sparrows (64 days), and Field Sparrows (64 days) and shortest for Dickcissels (51 days).

Clutch size decreased during the nesting season for Dickcissels ($t = -6.19$, df = 190, $P < 0.001$), Grasshopper Sparrows ($t = -2.23$, df = 130, $P = 0.03$), and Field Sparrows ($t = -5.52$, df = 259, $P < 0.001$). On average, Dickcissel clutch size was reduced by one egg every 50 days, and Grasshopper Sparrow and Field Sparrow clutch sizes were reduced by 0.5 eggs every 62 and 52 days, respectively. We did not detect a linear decrease in clutch size during the nesting season

for Henslow's Sparrow ($t = -0.37$, df = 104, $P = 0.71$) and Eastern Meadowlark ($t = -0.94$, df = 85, $P = 0.35$). The clutch size for both Henslow's Sparrows and Eastern Meadowlarks initially increased, peaked in the middle of the season, and then gradually decreased.

Nesting success was generally greatest for nests found during the laying stage and least during the incubation stage. Combining nests found in all years, nesting success for Field Sparrows was lower than for Grasshopper Sparrows because of the difference in nest success during the incubation stage (Table 2). Nesting success varied among years, but we were unable to detect differences after Bonferroni correction (Table 3).

DISCUSSION

Overall mean nesting success rates (Mayfield 1975) were within the range of values previously reported for Henslow's Sparrows (27% [incubation and nestling stages only]; Table 4), and Dickcissels (26%). Eastern Meadowlark (22%) and Grasshopper Sparrow (41%) nesting success was near the high end of previously reported values (Table 4). Almost all nests of these four species were found in the largest fields (>150 ha). A few Henslow's Sparrow nests were found in fields as small as 4 ha, but these small fields were within 10 km of larger fields. Henslow's Sparrow densities were too low in small fields to allow for an adequate sample of nests each year. Field Sparrow nesting success was lower at Fort Campbell (20%) than previously reported (Table 4). Low nesting success may be related to the ubiquitous distribution of Field Sparrow nests in grassland fields, including some fields as small as 2 ha. Smaller fields had more habitat features that might attract potential predators (e.g., small trees for perch sites), possibly accounting for reduced nesting success rates (Herkert 1994).

Published nesting success rates usually do not include the egg laying stage. Between 6 and 36% of our nests, depending upon species and year, were found during the egg laying stage. This study is one of only a few that explicitly reports a daily survival rate of nests during the laying stage. We detected nest failures for three of the five species monitored during this short but critical part of the nesting cycle, resulting in estimates of nest success during the egg-laying stage of 65–79%. The egg laying stage should be treated separately from the incubation stage because incubation usually starts between laying the penultimate egg and up to a few days thereafter. Eggs usually are less conspicuous when the female is on the nest during incubation, reducing the probability predators will find the nest through visual cues. Exposed eggs during the laying stage may be more vulnerable to predators such as common raccoons (*Procyon lotor*) or Blue Jays (*Cyanocitta cristata*). The laying stage tended to have the greatest nest success rates followed by the nestling stage and the incubation stage (Table 2).

Brown-headed Cowbird parasitism rates were low at Fort Campbell for these grassland species, but were within the range of reported parasitism rates for each species (Table 4). The lack of Dickcissel nest parasitism was particularly noteworthy when compared with other areas, but was consistent with records from Tennessee (Nicholson 1997). Our nest parasitism rates probably were low because most nests were in large grassland fields (>100 ha) far from forest edges or other tall woody perch sites (Hauber and Russo 2000, Jensen and Cully 2005), except those of Field Sparrows, which were found in the full range of field sizes (4–600 ha). Nest parasitism rates may be related to the proximity of songbird populations to the greatest densities of Brown-headed Cowbirds (Basili 1997, Winter et al. 2004). Fort Campbell is outside the greatest density areas for Brown-headed Cowbird populations (Sauer et al. 2004). Morris and Thompson (1998) found Brown-headed Cowbirds were most associated with grazed pastures, regardless of grass height. There is no livestock grazing activity at Fort Campbell.

Clutch sizes of Henslow's Sparrows, Grasshopper Sparrows, Dickcissels, and Eastern Meadowlarks were slightly greater at Fort Campbell than average but were within the range of published rates (Table 4). Field Sparrow clutch size was less than average, but within the range of published rates. Average clutch sizes included two nests with more than twice the average number of eggs, one Dickcissel with nine eggs and one Eastern Meadowlark with 10 eggs. These individual nests may represent egg laying efforts of more than

TABLE 2. Mayfield nesting success of grassland birds at Fort Campbell, Kentucky, 1999–2003, by nest cycle interval.

Species	Nest cycle interval[a]	Mean days in period[b]	n[c]	Failures (n)[d]	Exposure days[e]	Daily survival[f]	SE	Success (%)[g]
HESP[h]	Laying	4.0	8	2	19.5	0.897	0.069	64.9
GRSP	Laying	4.5	8	0	17.0	1.000	0.000	100.0
DICK	Laying	4.0	75	13	229.0	0.943	0.015	79.2
EAME	Laying	4.0	13	0	26.0	1.000	0.000	100.0
FISP	Laying	3.5	47	11	124.0	0.911	0.026	71.6
HESP	Incubating	11.0	54	21	297.5	0.929	0.015	44.7
GRSP	Incubating	11.5	73	23	445.0	0.948	0.010	54.3
DICK	Incubating	12.5	145	67	997.0	0.933	0.008	41.9
EAME	Incubating	12.5	54	25	354.5	0.929	0.014	40.1
FISP	Incubating	12.0	176	83	912.5	0.909	0.010	31.8
HESP	Nestling	9.5	88	23	412.5	0.944	0.011	58.0
GRSP	Nestling	9.0	108	23	621.0	0.963	0.008	71.2
DICK	Nestling	9.0	124	37	694.5	0.947	0.009	61.1
EAME	Nestling	9.0	61	25	387.0	0.935	0.012	54.8
FISP	Nestling	7.5	183	56	849.5	0.934	0.009	60.0
HESP	Inc. and nestling	20.5	111	44	710.0	0.938	0.009	26.9
GRSP	Inc. and nestling	20.5	129	46	1,066.0	0.957	0.006	40.5
DICK	Inc. and nestling	21.5	191	104	1,691.5	0.939	0.006	25.6
EAME	Inc. and nestling	21.5	86	50	741.5	0.933	0.009	22.3
FISP	Inc. and nestling	19.5	266	139	1,762.0	0.921	0.006	20.1
HESP	All stages	24.5	113	46	729.5	0.937	0.009	20.3
GRSP	All stages	25.0	129	46	1,083.0	0.958	0.006	33.8
DICK	All stages	25.5	204	117	1,920.5	0.939	0.005	20.1
EAME	All stages	25.5	86	50	767.5	0.935	0.009	17.9
FISP	All stages	23.0	276	150	1,886.0	0.920	0.006	14.7

[a] Nesting cycle intervals include laying, incubating, nestling, incubation and nestling combined, and all stages combined.
[b] Expected length (days) of each stage from Ehrlich et al. (1988).
[c] Number of nests monitored in each nest cycle interval.
[d] Total number of failed nests.
[e] Total number of exposure days (Mayfield 1975).
[f] Probability of daily nest success (Mayfield 1975).
[g] Probability of nest success (Mayfield) through the nesting cycle interval.
[h] HESP = Henslow's Sparrow, GRSP = Grasshopper Sparrow, DICK = Dickcissel, EAME = Eastern Meadowlark, FISP = Field Sparrow.

TABLE 3. Annual daily survival and nest success rates for grassland birds at Fort Campbell, Kentucky, 1999–2003.

Year	Rate	Henslow's Sparrow	Grasshopper Sparrow	Dickcissel	Eastern Meadowlark	Field Sparrow
1999	Days(n)[a]	25.5(6)	96.0(19)	111.0(14)	125.5(12)	150.5(23)
	DSR(SE)[b]		0.948(0.023)	0.910(0.027)	0.920(0.024)	0.907(0.024)
	Success		26.3	9.0	12.0	10.5
2000	Days(n)	276.5(40)	257.5(30)	324.0(40)	149.0(17)	522.5(84)
	DSR(SE)	0.920(0.016)	0.973(0.010)	0.935(0.014)	0.913(0.023)	0.912(0.012)
	Success	13.1	50.2	18.1	9.7	11.9
2001	Days(n)	235.5(26)	215.0(26)	755.5(74)	201.5(23)	536.0(71)
	DSR(SE)	0.958(0.013)	0.944(0.016)	0.943(0.008)	0.945(0.016)	0.920(0.012)
	Success	34.5	23.8	22.4	23.9	14.5
2002	Days(n)	116.0(20)	231.0(24)	311.0(30)	142.5(15)	298.0(47)
	DSR(SE)	0.940(0.022)	0.952(0.014)	0.949(0.013)	0.951(0.018)	0.906(0.017)
	Success	21.8	29.5	26.0	27.7	10.2
2003	Days(n)	77.5(20)	283.5(30)	419.0(46)	149.0(19)	379.0(51)
	DSR(SE)	0.948(0.025)	0.961(0.011)	0.936(0.012)	0.940(0.020)	0.950(0.011)
	Success	27.3	37.2	18.3	20.4	30.5

[a] Days = total exposure days, n = number of nests. Nest exposure includes laying, incubation, and nestling stages.
[b] DSR = Daily survival rate (Mayfield 1975).

TABLE 4. Weighted average and range of published demographic rates for Henslow's Sparrow, Grasshopper Sparrow, Field Sparrow, Eastern Meadowlark, and Dickcissel.

Species		Clutch size	Parasitized	Apparent success	Mayfield success[a]
Henslow's Sparrow[b]	Average[c]	3.8	0.03	0.51	0.29
	Range[d]	3.3–4.4	0.00–0.08	0.19–0.74	0.07–0.46
Grasshopper Sparrow[e]	Average	4.2	0.09	0.44	0.32
	Range	3.7–4.6	0.00–0.50	0.15–0.80	0.07–0.52
Dickcissel[f]	Average	4.0	0.40	0.48	0.26
	Range	3.7–4.7	0.03–0.95	0.46–0.67	0.12–0.50
Eastern Meadowlark[g]	Average	4.4	0.08	0.32	0.10
	Range	4.1–5.2	0.00–0.70	0.30–0.70	0.10–0.25
Field Sparrow[h]	Average	3.7	0.12	0.36	0.27
	Range	3.4–4.0	0.00–0.80	0.10–0.72	0.21–0.47

[a] Probability of nest success corrected for exposure time (Mayfield 1975).
[b] Robins 1971, Peck and James 1987, Winter 1998, Reinking et al. 2000, Monroe 2001, Burhans 2002.
[c] Average for published values weighted by sample size.
[d] Range of published average values.
[e] Price 1934, Elliot 1978, Wray et al. 1982, McNair 1987, Vickery et al. 1992, Winter 1998, Reinking et al. 2000, Balent and Norment 2003, Vos 2003, Giocomo 2005, Sutter and Ritchison 2005.
[f] Long 1963; Gross 1968; Elliot 1978; Zimmerman 1982, 1983; Basili 1997; Winter 1998; Vos 2003; Jensen and Finck 2004; Fletcher et al. 2006.
[g] Saunders 1932, Johnston 1964, Roseberry and Klimstra 1970, Elliot 1978, Peck and James 1987, Knapton 1988, Lanyon 1995, Granfors et al. 1996, Winter 1998.
[h] Hicks 1934, Walkinshaw 1939, Crooks 1948, Best 1978, Wray et al. 1982, Carey et al. 1994, Barber et al. 2001, Vos 2003.

one female each. Both nests were lost to predation before the eggs hatched, and we were not able to confirm the number of parents visiting the nest.

Grassland birds have relatively low nesting success, compensated by several nesting attempts within a single season (Wiens 1969, Martin 1995, Winter 1999). The length of the nest initiation window (51–75 days) suggests the possibility of multiple breeding attempts or multiple successful broods within a single breeding season for all five species. Henslow's Sparrows and Grasshopper Sparrows are generally considered at least double brooded; two pairs from a color-banded Henslow's Sparrow population in Kentucky had three successful broods in one season (Monroe 2001). Some nests initiated in July could represent third attempts or successful broods for some nesting pairs. The amount of time from the start of the nesting season (late Apr) and the last nests (early Aug) allows for the possibility of three broods if the time to finish a complete nesting cycle is less than 32 days including nest building (Ehrlich et al. 1988). Dickcissels are considered single brooded, or may move to a different location to re-nest (Winter 1998), but the nest initiation window for Dickcissels at Fort Campbell was sufficiently long to allow for the possibility of double brooding (51 days). Field Sparrows are considered double brooded, but their nesting success was so low at Fort Campbell that few pairs could produce two successful nests within the nesting season without many unsuccessful nesting attempts. Field Sparrows had sufficient time to complete at least two successful nests with several unsuccessful attempts (64 days).

The length of the nest initiation window for Eastern Meadowlarks at Fort Campbell was sufficiently long for three successful nesting attempts, but Eastern Meadowlarks may delay for a longer period between successive nests than expected. Kershner et al. (2004) radiotracked female Eastern Meadowlarks in Illinois and reported although they had time in the season to nest more than once, many birds did not re-nest in the same territory. This behavior would spread the distribution of nesting attempts across the season, and could account for the long nesting season for Eastern Meadowlark (75 days) in our study.

Clutch size decreased during the nesting season for Dickcissels, Grasshopper Sparrows, and Field Sparrows. The second brood would be reduced by about one for Dickcissels, and about 0.5 for Grasshopper Sparrows and Field Sparrows if these species were double brooded. Clutch size did not show a linear relationship with time of egg laying during the nesting season for Henslow's Sparrows and Eastern Meadowlarks. Winter (1998) also re-

ported a lack of relationship between clutch size and time in nesting season for Henslow's Sparrow. Eastern Meadowlarks and Henslow's Sparrows tended to have smaller clutch sizes at the beginning and end of the nesting season.

The fields monitored at Fort Campbell were used extensively for army training exercises, such as airborne-troop parachute drops and associated vehicle activity, throughout the breeding season for grassland birds. However, most (88%) recorded nest losses were attributed to predation and few (<1%) nests were affected directly by military activities. Vehicle or troop movements crushed a few nests. Mowing for hay and weather accounted for more recorded nest losses (3 and 1.7%, respectively) than military activities. Nest searching activities were concentrated in grasslands not managed specifically for hay production, and land management effects observed were not representative of all grasslands in the area. Undoubtedly, a much larger proportion of nests failed because of mowing in grassland fields managed for hay production. However, nest searching was concentrated in areas used extensively for military training, and nest failure rates may be considered representative of direct military training impacts at Fort Campbell.

ACKNOWLEDGMENTS

The Department of Defense Legacy Resource Management Program, Fort Campbell, and the University of Tennessee Agricultural Experiment Station sponsored this project. We thank the staff in the Conservation Branch at Fort Campbell for assistance with project logistics and the many field assistants who helped search for nests.

LITERATURE CITED

Askins, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. Current Ornithology 11:1–34.

Balent, K. L. and C. J. Norment. 2003. Demographic characteristics of a Grasshopper Sparrow population in a highly fragmented landscape of western New York State. Journal of Field Ornithology 74: 341–348.

Barber, D. R., T. E. Martin, M. A. Melchiors, R. E. Thill, and T. B. Wigley. 2001. Nesting success of birds in different silvicultural treatments in southeastern U.S. pine forests. Conservation Biology 15:196–207.

Basili, G. D. 1997. Continental scale ecology and conservation of the Dickcissel. Dissertation. University of Wisconsin, Madison, USA.

Best, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95:9–22.

Burhans, D. E. 2002. Conservation assessment for Henslow's Sparrow *Ammodramus henslowii*. USDA, Forest Service, General Technical Report NC-226. North Central Research Station, St. Paul, Minnesota, USA.

Carey, M., D. E. Burhans, and D. A. Nelson. 1994. Field Sparrow (*Spizella pusilla*). The birds of North America. Number 103.

Chester, E. W., B. E. Wofford, J. M. Baskin, and C. C. Baskin. 1997. A floristic study of barrens on the southwestern Pennyroyal Plain, Kentucky and Tennessee. Castanea 62:161–172.

Crooks, M. P. 1948. Field Sparrow life history in central Iowa. Iowa Bird Life 23:10–13.

Delcourt, P. A., H. R. Delcourt, D. F. Morse, and P. A. Morse. 1993. History, evolution, and organization of vegetation and human culture. Pages 47–80 *in* Biodiversity of the southeastern United States (W. H. Martin, S. G. Boyce, and A. C. Echternacht, Editors). John Wiley and Sons, New York, USA.

Eberly, C. 2002. Defending the stepping stones of migration. Birding 34:450–458.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook. Simon and Schuster Inc., New York, USA.

Elliot, P. F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. Auk 95:161–167.

Fletcher Jr., R. J., R. R. Koford, and D. A. Seaman. 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. Journal of Wildlife Management 70:145–157.

Giocomo, J. 2005. Grasshopper Sparrows nesting in eastern Tennessee. The Migrant 75:48–49.

Granfors, D. A., K. E. Church, and L. M. Smith. 1996. Eastern Meadowlarks nesting in rangelands and Conservation Reserve Program fields in Kansas. Journal of Field Ornithology 67:222–235.

Gross, A. O. 1968. Dickcissel. Pages 158–191 *in* Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and their allies (O. L. Austin, Editor). Part 1. U.S. National Museum Bulletin 237.

Hauber, M. E. and S. A. Russo. 2000. Perch proximity correlates with higher rates of cowbird parasitism of ground nesting Song Sparrows. Wilson Bulletin 112:150–153.

Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecological Applications 4:461–471.

Herkert, J. R., D. W. Sample, and R. E. Warner. 1996. Management of Midwestern grassland landscapes for the conservation of migratory grassland birds. Pages 89–116 *in* Management of Midwestern landscapes for the conservation of neotropical migratory birds (F. R. Thompson III, Editor). USDA, Forest Service, General Technical Report NC-187. North Central Research Station, St. Paul, Minnesota, USA.

HICKS, L. E. 1934. A summary of cowbird host species in Ohio. Auk 51:385–386.

JENSEN, W. E. AND J. F. CULLY JR. 2005. Density-dependent habitat selection by Brown-headed Cowbirds (*Molothrus ater*) in tallgrass prairie. Oecologia 142:136–149.

JENSEN, W. E. AND E. J. FINCK. 2004. Edge effects on nesting Dickcissels (*Spiza americana*) in relation to edge type of remnant tallgrass prairie in Kansas. American Midland Naturalist 151:192–199.

JOHNSON, R. G. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

JOHNSTON, R. F. 1964. The breeding birds of Kansas. Museum of Natural History. University of Kansas Publication 12:575–655.

KERSHNER, E. L., J. W. WALK, AND R. E. WARNER. 2004. Breeding-season decisions, renesting, and annual fecundity of female Eastern Meadowlarks (*Sturnella magna*) in southeastern Illinois. Auk 121:796–805.

KNAPTON, R. W. 1988. Nesting success is higher for polygynously mated females than for monogamously mated females in the Eastern Meadowlark. Auk 104:325–338.

LANYON, W. E. 1995. Eastern Meadowlark (*Sturnella magna*). The birds of North America. Number 160.

LONG, C. A. 1963. Production of sterile eggs in the Dickcissel. Wilson Bulletin 75:456.

MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101–127.

MARZLUFF, J. M. AND R. SALLABANKS. 1998. Past approaches and future directions for avian conservation biology. Pages 5–14 *in* Avian conservation: research and management (J. M. Marzluff and R. Salabanks, Editors). Island Press, Washington, D.C., USA.

MAYFIELD, H. 1961. Nest success calculated from exposure. Wilson Bulletin 73:255–261.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MCNAIR, D. B. 1987. Egg data slips—are they useful for information on egg-laying dates and clutch size? Condor 89:369–376.

MONROE, M. S. 2001. Reproductive success of Henslow's Sparrows in Kentucky: effects of season, nest characteristics, and vegetation structure. Thesis. Eastern Kentucky State University, Richmond, USA.

MORRIS, D. L. AND F. R. THOMPSON III. 1998. Effects of habitat and invertebrate density on abundance and foraging behavior of the Brown-headed Cowbird. Auk 115:376–385.

MOSS, E. D. 2001. Distribution and reproductive success of native grassland birds in response to burning and field size at Fort Campbell Military Reservation: special focus on Henslow's and Grasshopper sparrows. Thesis. University of Tennessee, Knoxville, USA.

NICHOLSON, C. P. 1997. Atlas of the breeding birds of Tennessee. University of Tennessee Press, Knoxville, USA.

PECK, G. AND R. JAMES. 1987. Breeding birds of Ontario: nidiology and distribution. Volume 2. Passerines. Miscellaneous Publications. Royal Ontario Museum of Life Sciences, Toronto, Ontario, Canada.

PETERJOHN, B. G. AND J. R. SAUER. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey 1966–1996. Studies in Avian Biology 19:27–44.

PRICE, H. F. 1934. A few cowbird notes. Oologist 51: 107–108.

REINKING, D. A., D. A. WIEDENFELD, D. H. WOLFE, AND R. ROHRBAUGH. 2000. Distribution, habitat use, and nesting success of Henslow's Sparrows in Oklahoma. Prairie Naturalist 32:219–232.

ROBINS, J. D. 1971. A study of Henslow's Sparrow in Michigan. Wilson Bulletin 83:39–48.

ROSEBERRY, J. L. AND W. D. KLIMSTRA. 1970. The nesting ecology and reproductive performance of the Eastern Meadowlark. Wilson Bulletin 82:243–267.

SAUER, J. R. AND J. E. HINES. 1989. Testing for differences among survival or recovery rates using program CONTRAST. Wildlife Society Bulletin 17: 549–550.

SAUER, J. R., J. E. HINES, AND J. FALLON. 2004. The North American Breeding Bird Survey, results and analysis 1966–2003. Version 2004.1. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. Online at ⟨http://www.mbr-pwrc.usgs.gov/bbs/bbs.html⟩ (accessed 1 February 2005).

SAUNDERS, G. B. 1932. A taxonomic revision of the meadowlarks of the genus *Sturnella* (Vieillot) and natural history of the Eastern Meadowlark, *Sturnella magna magna* (Linnaeus). Dissertation. Cornell University, Ithaca, New York, USA.

SUTTER, B. AND G. RITCHISON. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. Journal of Field Ornithology 76:345–351.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

VICKERY, P. D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*). The birds of North America. Number 239.

VICKERY, P. D., M. L. HUNTER, AND J. V. WELLS. 1992. Is density an indicator of breeding success? Auk 109:706–710.

VOS, S. M. 2003. Distribution, abundance, and productivity of grassland birds on Fort McCoy military base. Thesis. University of Wisconsin, Madison, USA.

WALKINSHAW, L. H. 1939. Nesting of Field Sparrow and survival of young. Bird-banding 10:107–114, 149–157.

WIENS, J. A. 1969. An approach to the study of eco-

logical relationships among grassland birds. Ornithological Monographs 8.

WINTER, M. 1998. Effect of habitat fragmentation on grassland-nesting birds in southwestern Missouri. Dissertation. University of Missouri, Columbia, USA.

WINTER, M. 1999. Nesting biology of Dickcissels and Henslow's Sparrows in southwestern Missouri prairie fragments. Wilson Bulletin 111:515–527.

WINTER, M., J. A. SHAFFER, D. H. JOHNSON, T. M. DONOVAN, W. D. SVEDARSKY, P. W. JONES, AND B. R. EULISS. 2004. Habitat and nesting of Le Conte's Sparrows in the northern tallgrass prairie. Journal of Field Ornithology 76:61–71.

WRAY II, T. K. A. STRAIT, AND R. C. WHITMORE. 1982. Reproductive success of grassland sparrows on a reclaimed surface mine in West Virginia. Auk 99: 157–164.

ZAR, J. H. 1998. Biostatistical analysis. Fourth Edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

ZIMMERMAN, J. L. 1982. Nesting success of Dickcissels in preferred and less preferred habitats. Auk 99: 292–298.

ZIMMERMAN, J. L. 1983. Cowbird parasitism of Dickcissels in different habitats at different nest densities. Wilson Bulletin 95:7–25.

The Wilson Journal of Ornithology 120(1):120–130, 2008

FACTORS AFFECTING HOME RANGE SIZE AND MOVEMENTS OF POST-FLEDGING GRASSLAND BIRDS

KIMBERLY M. SUEDKAMP WELLS,[1,3,4] JOSHUA J. MILLSPAUGH,[1] MARK R. RYAN,[1] AND MICHAEL W. HUBBARD[2]

ABSTRACT.—We describe post-fledging movements and evaluate the effects of local vegetation, temporal, and biological factors on home range size for two species of declining grassland birds in southwestern Missouri from 2002 to 2004. We obtained ≥30 detections for 74 individual juvenile Dickcissels (*Spiza americana*) and 64 juvenile Eastern Meadowlarks (*Sturnella magna*) during the post-fledging period. Juvenile Eastern Meadowlarks had a greater total number of days (6.7 ± 0.6) with large (>300 m) movements than juvenile Dickcissels (5.0 ± 0.5 days). Average Dickcissel home range size was larger and three times as variable in 2002 (77.0 ± 22 ha) compared to 2003 (31.4 ± 7.5 ha) and 2004 (34.9 ± 7.5 ha). There were year-specific effects of the variability in vegetation height on home range size of juvenile Dickcissels. Home range size was similar among years for juvenile Eastern Meadowlarks (2002, 109.4 ± 39.2 ha; 2003, 82.7 ± 29.4 ha; 2004, 70.7 ± 11.6 ha), but there was a year-specific effect of variability in grass cover on home range size of juvenile Eastern Meadowlarks. Local vegetation conditions are important factors affecting home range size and movements during the post-fledging period. *Received 28 August 2006. Accepted 28 March 2007.*

The post-fledging period is widely recognized as the least understood portion of the avian life cycle (Baker 1993), primarily due to constraints associated with monitoring juveniles during natal dispersal (Greenwood and Harvey 1982). Natal dispersal typically includes the period between the time a juvenile fledges and returns to breed the following year as an adult (Greenwood and Harvey 1982). During the post-fledging period (a subset of the natal dispersal period), defined as the period between fledging and departure for migration or settling in wintering areas (Anders et al. 1998), juveniles become independent from parents and develop flight and foraging skills. Simultaneously, juveniles must also learn to avoid predators and cope with adverse weather conditions that shape components of post-fledging dispersal such as movement patterns. Movement patterns may subsequently influence population dynamics by affecting the probability of juvenile survival (Magrath 1991, Cohen and Lindell 2004, Kershner et al. 2004, Wiens et al. 2006, Yackel Adams et al. 2006), resource selection (Anders et al. 1998, Vega Rivera et al. 1998, Kennedy and Ward 2003, Berkeley 2005), recruitment (Green and Cockburn 2001), genetic structure (Dingemanse et al. 2003), and breeding dispersal as an adult (Kenward et al. 2001). Thus, describing post-fledging dispersal and potential factors affecting movement patterns is important for developing bird conservation strategies.

Vegetation, temporal, and biological factors are the dominant hypotheses that have been used to explain movement patterns during the post-fledging period. Local vegetation conditions may be important for providing site-selection cues associated with food availability or protection from predators. For example, juvenile Northern Goshawks (*Accipiter gentilis*) that received supplemental food on their natal territories had earlier onset of dispersal movements from the natal area and no permanent dispersal from the study area compared to control birds (Kennedy and Ward 2003). Vegetation structure has also been shown to be an important local-scale factor affecting movements of juvenile Dickcissels (*Spiza americana*) that seek favorable vegetation conditions for maximizing concealment from predators (Berkeley 2005). Temporal factors, such as year-specific trends in weather conditions, have also been associated with movement patterns of Lark Buntings (*Calamospiza melanocorys*) during the post-fledging period (Yack-

[1] Department of Fisheries and Wildlife Sciences, University of Missouri–Columbia, Columbia, MO 65211, USA.

[2] Resource Science Division, Missouri Department of Conservation, Jefferson City, MO 65102, USA.

[3] Current address: H.T. Harvey & Associates, 983 University Avenue, Building D, Los Gatos, CA 95032, USA.

[4] Corresponding author; e-mail: kwells@harveyecology.com

el Adams et al. 2001). Individual or cohort-level biological factors are the third major hypothesis associated with movements during the post-fledging period. Juvenile Greater Flamingos (*Phoenicopterus roseus*) in good body condition had a higher probability of movement during the post-fledging period than juveniles in poor body condition (Barbraud et al. 2003). Low nestling rank or body mass has also been associated with higher dispersal probabilities in juvenile House Sparrows (*Passer domesticus*) that were in poor condition compared to nestlings of higher rank or body mass (Altwegg et al. 2000).

We describe home range size and daily movement patterns during the post-fledging period for two species of declining, grassland songbirds: Dickcissel and Eastern Meadowlark (*Sturnella magna*). Both are grassland-breeding songbirds that have shown regional and national declines over the last several decades (Sauer et al. 2005). Dickcissels are also on the Partners in Flight Continental Watchlist as a species of conservation concern (Rich et al. 2004). We were interested in home range size and daily movement patterns of these species because both aspects of the post-fledging period are largely undescribed for grassland birds. Our specific objectives were to: (1) compare daily movements of both species, (2) estimate home range size, and (3) model the effects of vegetation, temporal, and biological factors on home range size.

METHODS

Study Area.—We conducted the study at Taberville Conservation Area (38° N, 93° W) and Wah'Kon-Tah Prairie (37° N, 94° W) in Cedar and St. Clair counties in southwestern Missouri. Taberville Conservation Area is a 680-ha prairie owned and managed by the Missouri Department of Conservation (MDC). Wah'Kon-Tah Prairie is a 1,930-ha prairie at the northern periphery of El Dorado Springs, Missouri. It is owned by the Missouri Chapter of The Nature Conservancy (TNC), and jointly managed by MDC and TNC. Both sites are similar and embedded in an agricultural matrix of crops (wheat, soybeans, and corn) and grazing lands (pasture, hay fields) on surrounding private property. Dominant land management practices on both sites include livestock grazing, prescribed burning, seed harvesting for native plants, and hay production. The study sites are divided into units that receive management (primarily prescribed burning or mowing) applied by the same MDC personnel at least once every 3 years. Dominant vegetation is native grasses including big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), and Indian grass (*Sorghastrum nutans*). Forb species include coneflowers (*Echinacea* spp.), white wild indigo (*Baptisa alba*), blazing star (*Liatrus* spp.), compass plant (*Silphium laciniatum*), milkweeds (*Aesclepias* spp.), and sunflowers (*Helianthus* spp.). Woody species include smooth sumac (*Rhus glabra*), persimmon (*Diospyros virginiana*), blackberry (*Rubus* spp.), and roses (*Rosa* spp.). The average annual precipitation is 102 cm with most occurring during the growing season between April and August (Missouri Climate Center 2005). Fall 2002 marked the start of a severe drought that lasted into summer 2003 and was the most severe drought on record in the last two decades.

Bird Handling and Marking.—We located nests of both species using systematic searches and focused surveys in areas with Dickcissels and Eastern Meadowlarks, and appropriate nesting vegetation. We conducted nest searches every day from 0600 to 1400 hrs CDT during the nesting season between the third week of April and the second week of August from 2002 to 2004. We used behavioral cues of parents to indicate the presence of a nest. We recorded GPS coordinates and marked the location of each nest by placing colored flagging tape at least 5 m distant. We recorded the species, content, and parental activity at each nest. If the nest contained nestlings, we attempted to classify their age based on presence of down feathers, whether eyes were open or not, extent of pin feather development, or presence of a full complement of feathers (KSW, unpubl. data) as well as published information (Eastern Meadowlarks only; Lanyon 1995). We monitored each nest every 3–4 days until 2–3 days prior to the expected fledging date and then switched to daily nest checks. We attached a metal USGS band to the left leg and a unique combination of plastic, UV-resistant Darvic bands (Avinet, Dryden, NY, USA) to the right leg 2–3 days prior to fledging (6–7 days of age for Dick-

cissels; 9–11 days of age for Eastern Meadowlarks), and weighed each individual to the nearest gram using a spring scale (Avinet, Dryden, NY, USA).

We modified the Rappole and Tipton method (1991) (Suedkamp Wells et al. 2003) and attached 0.7-g transmitters with a 10-cm whip antenna (Biotrack, Dorset, UK) to the back of each bird using a leg harness. We constructed the leg harness from cotton, elastic beading cord to allow room for growth. Battery life for each transmitter was expected to range between 55 and 60 days. We secured the bottom of the transmitter to the back of the bird using super glue (Duro, Avon, OH, USA) and placed nestlings back in the nest. Forced fledging was occasionally observed during the beginning of the study in 2002, but modification of our protocol by attaching transmitters to younger nestlings minimized subsequent forced fledging events. We generally attached transmitters to every member of a brood because prior experience during a pilot effort indicated we would have insufficient sample sizes if we only selected one individual per nest (KSW, pers. obs.). Inclusion of more than one sibling per brood may artificially appear to reduce variability, but empirical evaluations have demonstrated that random subsampling of multiple individuals within a cohort does not improve the precision or accuracy of home range estimates or their associated variability with kernel estimators (De Solla et al. 1999). We also demonstrated elsewhere that juvenile survival estimates for multiple individuals from the same brood are independent (KSW, unpubl. manuscript) Thus, we assumed home range sizes from individuals in the same brood were also independent. Handling and processing time usually was between 2–5 min per bird.

Radiotracking.—We began radiotracking birds using homing techniques (Mech 1983) the day after attaching transmitters. We were successful at obtaining visual locations of each bird during a tracking attempt at least 90% of the time (Suedkamp Wells 2005). We returned each subsequent morning if the brood remained in the nest and began tracking when at least one brood member fledged. Our goal was to track at least 25 individuals of both species for a minimum of 50 detections each nesting season (Garton et al. 2001). Initially we located each juvenile twice each day. We reduced tracking to one attempt per day after obtaining at least 50 detections of an individual within the post-fledging season to accommodate tracking more individuals during peak nesting periods. We systematically located juveniles during four daily time blocks corresponding to key periods of biological activity. The four tracking blocks were early morning (0600–0930 hrs), mid-morning (0930–1230 hrs), afternoon (1230–1700 hrs), and evening (1700–2130 hrs). We alternated among the four time periods during each tracking day to obtain two detections per day, one each in non-consecutive detection time periods. We avoided tracking before 0600 hrs and after 2130 hrs to reduce risk of stepping on juveniles when they could not be visually located.

We tracked each individual until we recovered the transmitter (with or without a carcass) through the end of August each post-fledging season. We performed extensive searches of the immediate area on foot immediately after being unable to locate an individual. If unsuccessful, we broadened the search to include all roads within a 3-km radius of the last known location and study site boundaries. We attempted to locate missing birds from aerial searches of 5 km strips over the study area in a helicopter twice monthly between 1 June and 30 August each year.

Statistical Analyses.—We restricted our sample of marked juveniles to those individuals with ≥30 detections for subsequent analyses because simulation research has indicated 30 is the minimum sample size required for stable home range estimates using kernel estimators (Seaman et al. 1999). We calculated the distance moved between locations using GPS coordinates from tracking sessions for each individual in the Animal Movements extension (Hooge and Eichenlaub 2000) of ArcView 3.3 (Environmental Systems Research Institute, Redlands, CA, USA). We calculated average daily movements by classifying each tracking event by age (days since fledging) of the juvenile and then averaging within age classes across individuals. We extracted the first age that each individual had daily movements >300 m and the total number of days with movements >300 m. We used 300 m as a threshold because visual inspection of average daily distances moved for

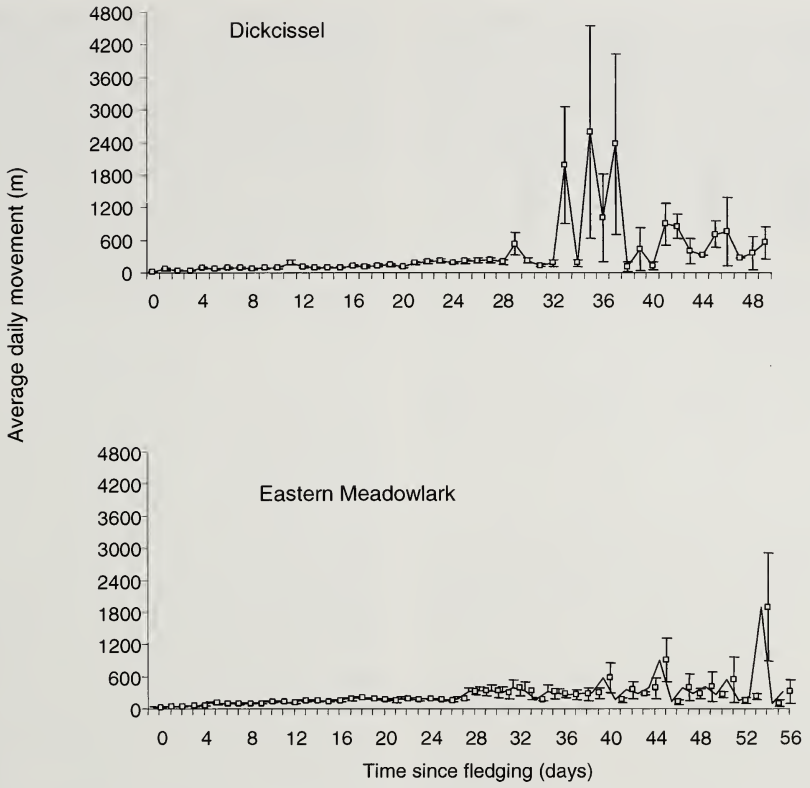


FIG. 1. Average (± SE) daily movements (m) for juvenile Dickcissels (n = 74) and Eastern Meadowlarks (n = 64) for individuals with ≥30 detections in southwestern Missouri, 2002–2004.

both species indicated relatively consistent trends in point estimates and their standard errors until movements exceeded this threshold (Fig. 1). We used two-sample t-tests in SYSTAT (SPSS 1999) to compare the first age that juveniles of both species showed daily movements exceeding 300 m and the total number of days where daily movements exceeded 300 m. We also included reference to large movements (>600 m) because these movements were associated with biologically meaningful periods such as flocking with other juveniles of the same species. We describe average daily movements for comparison with other published studies that commonly include movement parameters and because we were interested in fine-scale movements that comprise the home range estimate. We elected not to evaluate year effects on average daily movements because they represent a non-independent subset of all movements used to estimate home range size for an individual. We used an alpha level of 0.05 to infer significant results.

We calculated 95% home range contours using a fixed-kernel estimator (Worton 1987, 1989) from the 'KDE folder' (Beardah and Baxter 1995) in MATLAB (Mathworks 1999). Kernel estimators are favored for home range estimates because they are superior to several other methods (Kernohan et al. 2001). We used the "plug in" method and smoothed the x and y coordinates independently for the fixed-kernel estimator (Wand and Jones 1995, Jones et al. 1996). We tested for year effects on home range size using 95% confidence intervals.

We reduced multicollinearity and tested whether assumptions were violated with each explanatory factor prior to analysis. We used probability plots in SYSTAT to assess the distribution of each variable. We applied a log transformation for percent data (grass or forb cover) and a square root transformation for all

other variables if we detected evidence of non-normality (Steel et al. 1997). We used a data reduction approach in SYSTAT to detect potential problems with multicollinearity by visually inspecting scree plots from the Principal Components Analysis (PCA). We removed all variables except the most highly correlated variable for subsequent analyses of the reduced data set if multiple variables were highly correlated with the first PCA axis and did not contribute unique information based on visual inspection.

We used the General Linear Model module in SYSTAT to evaluate the effects of local vegetation, temporal, and biological factors on home range size with the reduced data set. Local vegetation factors included vegetation height (cm), grass cover (%), and forb cover (%) measured in a 20 × 50 cm Daubenmire frame (Daubenmire 1959) at each tracking location for each individual. We selected these variables *a priori* because prior analyses indicated they were important predictors of juvenile resource selection (Suedkamp Wells 2005). Other habitat features, such as woody cover, were also important for micro-scale resource selection (Suedkamp Wells 2005), but less appropriate for this analysis because patterns of variability were negligible when averaged across all movement locations used to generate home range size for an individual. We used the CV instead of average values of local vegetation variables because prior habitat selection analyses showed variability in vegetation structure was more important and most appropriately reflected the patchy environment of grassland vegetation (Suedkamp Wells 2005). We included temporal effects of year (2002–2004) because prior analyses demonstrated year-specific variability in home range size (Suedkamp Wells 2005). We did not include site as a temporal factor because prior analyses indicated large-scale differences in resource selection were weak and that within-site variability was more important than variability across sites (Suedkamp Wells 2005). Biological factors included juvenile body mass (g) at time of transmitter attachment, maximum observed clutch size (range 1–5 for both species), maximum number of siblings observed (range 1–5), and order of fledging (coded 1 for first fledging event and 2 for subsequent fledging events). Tracking recently fledged juveniles twice daily allowed us to record first and second fledging bouts, but our resolution was coarse because we were unable to differentiate order of fledging among juveniles that fledged after the second bout. We fit single parameter models and biologically meaningful interactions to the reduced data set. We used 95% confidence intervals to elucidate the simple effects driving the interaction if significant interactions were present.

RESULTS

Sample Description.—We located 258 Dickcissel nests and 113 Eastern Meadowlark nests during the 3-year study period. Average (± SE) clutch and brood sizes were 4.1 ± 0.9 eggs and 2.9 ± 1.3 nestlings for Dickcissels, and 4.4 ± 1.0 eggs and 3.3 ± 1.1 nestlings for Eastern Meadowlarks. We attached radio transmitters to 248 Dickcissel nestlings from 94 broods and 164 Eastern Meadowlark nestlings from 46 broods. Juveniles of both species generally transitioned to independence at 2–3 weeks of age after beginning gradual movements from the natal site. The subset of individuals with at least 30 detections used for subsequent home range and movement analyses included 74 juvenile Dickcissels (2002, $n = 25$; 2003, $n = 19$; 2004, $n = 30$) and 64 juvenile Eastern Meadowlarks (2002, $n = 8$; 2003, $n = 26$; 2004, $n = 30$). Individuals with ≥30 detections reflected the full range of brood sizes (1–5 nestlings) for both species in 2002 and 2004, but did not include the larger brood sizes for Dickcissels (4–5 nestlings) in 2003. Average nestling body mass at time of marking for Dickcissels with >30 detections (15.3 ± 0.4 g; 95% CI 14.6–16.0 g) was comparable to individuals with transmitters but with <30 detections (14.7 ± 0.4 g; 95% CI 14.0–15.4 g). Average nestling body mass for juvenile Eastern Meadowlarks was also similar for individuals with >30 detections (44.9 ± 0.8 g; 95% CI 43.3–46.5 g) and <30 detections (44.8 ± 1.3 g; 95% CI 42.2–47.5 g). Mortality during the first 2 weeks out of the nest was high with only 56% of juvenile Dickcissels and 57% of juvenile Eastern Meadowlarks surviving. The mean date of fledging (day zero out of the nest) was 25 June ± 1 day (range 5 Jun–24 Jul) for Dickcissels and 5 June ± 2 days (range 7 May–23 Jul) for

Eastern Meadowlarks with ≥30 detections per individual. The average number of detections per individual with at least 30 detections was 58.0 ± 1.2 (range 34–75) and 53.8 ± 1.1 (range 30–88) respectively, for Dickcissel and Eastern Meadowlark juveniles.

Movements.—Average daily movements by juvenile Dickcissels were relatively consistent although increasing at a slow rate until 28 days post fledging, which corresponds to the first 2 weeks of independence. Dickcissels had large daily movements (>600 m) starting at 28 days of age (Fig. 1). The period of largest movements occurred between days 32 and 38. Juvenile Eastern Meadowlarks also had slow but consistently increasing rates of daily movement until day 28. Juvenile Eastern Meadowlarks after day 28 had slightly larger movements and had three isolated peaks of large movement (>600 m) around days 40, 44, and 54 (Fig. 1). Peaks of large movements corresponded with altered periods of activity for juvenile meadowlarks when large daily movements were more characteristic as juveniles began congregating with other juvenile meadowlarks in roving flocks. Juveniles of both species frequently foraged or moved into surrounding private land beginning at 3–4 weeks of age.

The mean age that juveniles had daily movements >300 m was similar for Dickcissels (17.7 ± 1.4 days) and meadowlarks (20.1 ± 1.4 days; $P = 0.20$). The total number of days with daily movements >300 m differed between Dickcissel (5.0 ± 0.5 days) and Eastern Meadowlark (6.7 ± 0.6 days) juveniles ($P = 0.020$). The majority of juvenile Dickcissels (62%, $n = 46$) had 8 or fewer days with daily movements >300 m (Fig. 2). The peak of daily movements >300 m occurred between days 4 and 8 for most juvenile Eastern Meadowlarks (41%, $n = 26$) and the distribution of individuals in each category decreased more slowly compared to Dickcissel juveniles (Fig. 2).

Home Range Size.—Preliminary data reduction for Dickcissels with PCA showed that order of fledging ($r^2 = 0.59$), clutch size ($r^2 = 0.77$), and number of siblings ($r^2 = 0.85$) were highly correlated in order of increasing magnitude. Therefore, we removed order of fledging and clutch size from subsequent analyses to reduce multicollinearity. The reduced data

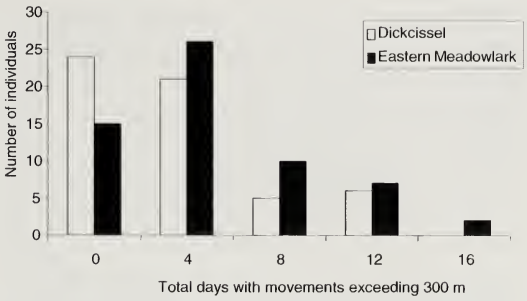


FIG. 2. Total number of days with large movements (≥300 m) for juvenile Dickcissels ($n = 74$; open bars) and Eastern Meadowlarks ($n = 64$; filled bars) with ≥30 detections in southwestern Missouri, 2002–2004.

set was tested for several single parameter effects (juvenile body mass, number of siblings, year, forb cover CV, and vegetation height CV) and two interactions (year and forb cover CV, year and vegetation height CV). Average Dickcissel home range size was larger and at least three times as variable in 2002 (77.0 ± 22.1 ha; 95% CI 31.3–122.6 ha) compared to 2003 (31.4 ± 7.5 ha; 95% CI 15.7–47.0 ha) and 2004 (34.9 ± 7.5 ha; 95% CI 19.6–50.2 ha). However, 95% confidence intervals overlapped across years indicating home range sizes were not statistically different. Average home range size pooled across years was 48.8 ± 8.8 ha. There was a significant ($P = 0.018$) interaction between year and the CV of vegetation height, which explained a large amount of variation in Dickcissel home range size (multiple $R^2 = 0.54$). The average CV of vegetation height for Dickcissels was higher and twice as variable in 2003 (0.59, 95% CI 0.49–0.69) compared to 2002 (0.40, 95% CI 0.36–0.45) and 2004 (0.47, 95% CI 0.43–0.51) based on non-overlapping 95% confidence intervals. The relationship between Dickcissel home range size and vegetation height CV varied more by home range size than vegetation height CV in 2002. This indicated the range of vegetation heights selected by juvenile Dickcissels during post-fledging dispersal was relatively consistent but associated with larger home ranges (Fig. 3). However, Dickcissel home ranges in 2003 and 2004 were characterized by a wider range of vegetation heights, indicating juveniles were selecting more variable vegetation heights that

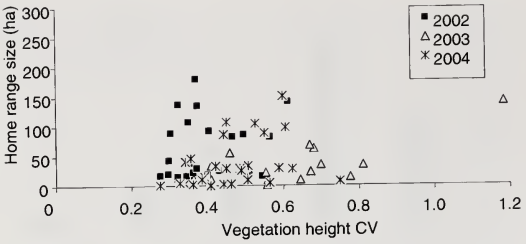


FIG. 3. Home range size (95% fixed kernel) for juvenile Dickcissels (n = 74) as a function of vegetation height CV and year (2002, filled squares; 2003, open triangles; 2004, asterisks) for individuals with ≥30 detections in southwestern Missouri.

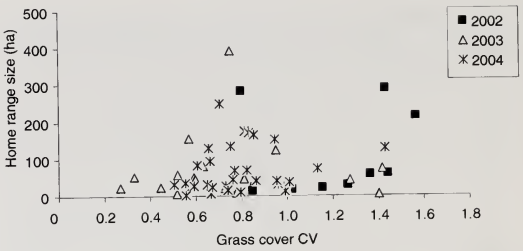


FIG. 4. Home range size (95% fixed kernel) for juvenile Eastern Meadowlarks (n = 64) as a function of grass cover CV and year (2002, filled squares; 2003, open triangles; 2004, asterisks) for individuals with ≥30 detections in southwestern Missouri.

may have facilitated smaller home ranges (Fig. 3).

Preliminary PCA results for Eastern Meadowlarks indicated that order of fledging (r^2 = 0.22), number of siblings (r^2 = 0.59), and clutch size (r^2 = 0.71) were correlated in increasing order of magnitude and we removed the former two variables from subsequent analyses to reduce multicollinearity. The correlation between order of fledging and the other two variables was lower than the other variables removed, but visual inspection of the scree plot indicated order of fledging did not contribute additional information. The reduced data set was tested for effects of several single parameters (juvenile body mass, clutch size, year, grass cover CV, and vegetation height CV) and several interactions (year and grass cover CV, year and vegetation height CV). Patterns of home range size for Eastern Meadowlarks were similar across years (2002, 109.4 ± 39.2 ha, 95% CI 19.0–199.8 ha; 2003, 82.7 ± 29.4 ha, 95% CI 22.2–143.2 ha; 2004, 70.7 ± 11.6 ha, 95% CI 47.0–94.5 ha) indicated by overlapping 95% confidence intervals, but variability decreased with successive years and increasing sample sizes in the study. Average home range size pooled across years was 80.9 ± 13.9 ha. There was a significant (P = 0.030) interaction between year and the CV of grass cover, which explained a large proportion of the variation in Eastern Meadowlark home range size (multiple R^2 = 0.56). The mean CV of grass cover was higher and twice as variable in 2002 (1.21, 95% CI 1.00–1.42) compared to 2003 (0.74, 95% CI 0.62–0.85) and 2004 (0.79, 95% CI 0.71–0.86). The relationship between home range size and the CV of grass cover in 2002 varied more by the CV of grass cover, indicating juvenile Eastern Meadowlarks were selecting a wider range of grass cover than was associated with larger home range sizes (Fig. 4). In contrast, juvenile Eastern Meadowlarks in 2003 and 2004 selected a narrower range of grass cover than was associated with smaller home range sizes. However, limited sample sizes in the first year (2002, n = 9) likely influenced the variability in home range size.

DISCUSSION

Movement Patterns.—Daily movement patterns for Dickcissels were not consistent with other studies, but daily movement patterns for Eastern Meadowlarks were consistent with other studies. Daily movement patterns for juvenile Dickcissels were consistently smaller than estimates for juvenile Lark Buntings, a similar-sized grassland bird in shortgrass prairies (Yackel Adams et al. 2001). Three weeks after fledging, average daily movements by Lark Buntings (238.5 ± 56.1 m) were still ~ 70% greater than those of juvenile Dickcissels (172.6 ± 21.8 m) despite comparable average body masses (Dickcissels, 15.3 ± 0.4 g; Lark Buntings, 21.4 ± 0.5 g). We would not predict large differences in daily movements between these two similarly sized species with similar ecological niches but drought conditions in the Colorado study or differences in landscape structure may have been responsible. Daily movements by Eastern Meadowlarks in our study were similar to patterns for the same species in highly fragmented grasslands in Illinois reported by Kershner et al. (2004).

Juvenile Meadowlarks at 2 weeks of age, in

our study had movements ranging between 100 and 150 m on average, which is similar to the range of movements between 100 and 120 m on average in Kershner et al.'s (2004) study. Juvenile meadowlarks in both studies were also reported foraging and using private land, particularly agricultural crops. Although fine-scale movement distances for this species were similar between studies in fragmented landscapes in the Midwest, additional information on this species and other grassland birds that reflects a range of landscape fragmentation is needed.

Patterns of average daily movement between species were somewhat surprising given their differences in body size (Dickcissels, 15.3 ± 0.4 g; Eastern Meadowlarks, 44.9 ± 0.8 g) and territory size (Dickcissel range = 0.16 to 1.10 ha, Zimmerman 1966, Harmeson 1974; Eastern Meadowlark range = 1.2 to 6.1 ha, Lanyon 1995). Greenwood and Harvey (1982) recommended framing natal dispersal distances as territory size to reflect potential biological constraints on dispersal distances. We would have expected juvenile Eastern Meadowlarks to have larger average daily movements at an earlier age and a higher total number of days with large movements compared to Dickcissel juveniles. Our results were only consistent with our prediction that larger, juvenile Eastern Meadowlarks would show a greater total number of days with large movements (>300 m). Our observations suggest the greater number of days with large movements for Eastern Meadowlarks may be associated with land use patterns and associated availability of food resources. For example, while nest searching we frequently observed female Eastern Meadowlarks repeatedly traveling >500 m from their nests to forage on private land outside our study areas where sweet clover (*Melilotus* spp.) was abundant. Later, the same females were frequently observed leading their broods to these food sources. Soon after juveniles left our study areas for private lands, we observed the initiation of larger daily movements and the formation of loose, conspecific flocks that made tracking more difficult. Several authors have reported similar observations for juvenile meadowlarks (Kershner et al. 2004) and juvenile Wood Thrush (*Hylocichla mustelina*) (Vega Rivera et al. 1998). Flock formation may be an adaptive strategy by juveniles to collectively reduce the risk of predation and share information about potential foraging sites in fragmented agricultural landscapes. Future research describing flock formation would be helpful for understanding selective pressures that influence dispersal of older juveniles as they begin navigating novel landscapes.

Home Range Size.—This is the first study, to our knowledge, to describe home range size for post-fledging grassland birds. Differences in average home range size across species (Dickcissels, 48.8 ± 8.9 ha; Eastern Meadowlarks, 80.9 ± 13.9 ha) reflect differences in body size and reported territory sizes. Previous studies on area sensitivity have suggested 50 ha is an appropriate minimum for many grassland birds (Herkert 1994, Helzer and Jelinksi 1999, Winter and Faaborg 1999), which encompasses the smaller of the two average home range sizes in our study. Both species in our study have been reported to be area sensitive (Herkert 1994, Helzer and Jelinski 1999, Winter and Faaborg 1999), indicating they are less likely to occur and potentially reproduce successfully in small patches compared to large patches. Future studies investigating the relationship between minimum area sizes required by adults and post-fledging juveniles would be helpful for incorporating all phases of the avian life history cycle into guidelines for grassland conservation and planning efforts.

Our finding that local vegetation and year-specific weather factors influence post-fledging dispersal is consistent with other studies of grassland birds (Kershner et al. 2004, Berkeley 2005, Yackel Adams et al. 2006). Home range sizes of juvenile Dickcissels in our study were larger when average vegetation height was shorter and less variable (as indicated by the CV), emphasizing the importance of taller grass and more variability in structural heterogeneity in grassland environments for this species. Dickcissels are considered a tallgrass prairie species and are frequently associated with taller plant heights characteristic of tallgrass prairie communities (Zimmerman 1966, Winter 1999, Suedkamp Wells 2005).

We believe the interaction between year and CV of vegetation height on home range size

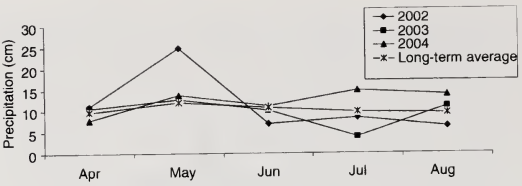


FIG. 5. Average precipitation by month of the growing season (Apr–Aug) and year (2002, filled diamonds; 2003, filled squares; 2004, filled triangles) for study sites in southwestern Missouri. The long-term average over 30 years (asterisks) is depicted for comparison (Missouri Climate Center 2005).

for juvenile Dickcissels was driven by abnormal patterns of precipitation early in the breeding season in 2002 (Fig. 5) and drought conditions in 2003 (Missouri Climate Center 2005). The 2002 growing season was unusual because twice the normal precipitation occurred in May, which triggered flooding that resulted in standing water and colder than normal conditions. May is a critical time for breeding pairs because females begin arriving in Missouri during the first week of May and initiate their first nesting attempts during the second week of May (KSW, pers. obs.). Dickcissels are normally assumed to be single brooded and females which lost or abandoned their nests in the storm may have renested in poor condition. This may have influenced subsequent brood sizes and their respective condition, which may influence their ability to disperse. However, we were unable to detect potential effects of clutch size or nestling body mass on home range size. Potential differences may have been more pronounced if we were able to compare seasonal reproductive effort between females which were successful with their first attempt and those that renested.

The variability of vegetation height (as indicated by the CV) within Dickcissel home ranges in 2003 was nearly twice the 2002 and 2004 averages. This pattern indicates the persistent drought that started in 2002 and continued through summer 2003 affected local vegetation structure by altering the types of vegetation present (forb vs. grass) and the resulting vegetation height. The absence of large broods (4–5 nestlings) of Dickcissels from our sample in 2003 may reflect the energetic strain on breeding females during prolonged drought periods when food is scarce due to limited availability of preferred substrates for dominant insect foods (e.g., forbs) (KSW, unpubl. data). One explanation for the change in vegetation height is that the early pulse of spring rain in April 2003 may have favored growth of forbs that typically compete with grasses for light and moisture, and provide important substrates for dominant insect foods. If grasses were physiologically stressed from the drought that started at the end of the 2002 growing season (Missouri Climate Center 2005), a competitive release in 2003 may be a viable explanation. Results from microhabitat selection by juvenile Dickcissels in companion parts of this study indicate the availability of grasses and forbs increased in 2003 compared to 2002 and the forb increase was proportionately larger (Suedkamp Wells 2005). This shift in dominant plant groups supports our explanation for the effects of drought on average vegetation height.

Local vegetation and year-specific factors also affected home range size for juvenile Eastern Meadowlarks. Interactions between year and the variability in grass cover (as indicated by the CV) were driven by patterns of grass composition that were twice as variable in 2002 versus 2003 and 2004. Results from a companion part of this study indicated the transition from 2002 to 2003 was associated with a two-fold increase in grass cover selected by juvenile Eastern Meadowlarks, despite similar levels of availability (Suedkamp Wells 2005). Grass cover was an important predictor of the presence of juvenile Eastern Meadowlarks in 2002 but not 2003 (Suedkamp Wells 2005), indicating grass cover was a more limiting habitat feature in 2002 versus 2003. Grass cover is important for breeding habitat because females typically build nests at the base of grass clumps and use litter to construct a roof and two side walls (KSW, pers. obs.).

CONSERVATION IMPLICATIONS

Our results provide support for the hypothesis that local vegetation factors primarily affect post-fledging dispersal of grassland birds. Conservation planners need realistic guidelines for grassland acquisition and management that incorporate adult and juvenile life history needs on public and private land if declining grassland bird populations are to be

stabilized. Our results coupled with previous recommendations demonstrate the importance of using minimum area requirements as the threshold for grassland acquisition and management plans that address all life history stages. Grassland managers should be aware that larger areas are required for species with larger body and territory sizes, such as meadowlarks, Upland Sandpipers (*Bartramia longicauda*), and Greater Prairie-chickens (*Tympanuchus cupido*) that are also present and species of conservation concern (Missouri Department of Conservation 2007). Home range sizes may be manipulated by managing for structural heterogeneity, which should reduce the minimum area required for both species in our study. Conservation planners should select and use management practices (prescribed burning, herbicides, grazing, mowing) to obtain the minimum required amounts of critical habitat components (vegetation height and grass cover in this case). Minimum area requirements may be affected by the relative proportion of public and private land within an individual or population home range. The majority of birds in this study left public lands and spent large periods of time on surrounding private lands, which is managed primarily for row crops and livestock grazing. The landscape context around public land may be equally important and must be considered when evaluating land acquisition and management plans for grassland birds to insure the necessary resources exist within appropriate distances for dispersing juveniles.

ACKNOWLEDGMENTS

We thank Frank Thompson, John Faaborg, Eric Bollinger, Maiken Winter, and David Sample for comments on earlier drafts that improved the manuscript. The Missouri Department of Conservation, and the University of Missouri USGS Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, and Conservation Biology Fellowship Program provided funding. Jason Wells provided assistance with data manipulation in Access. Len Gilmore, Kristin Austin, Sharon Gough, Jay Bowmaster, and Josh Cussimanio provided housing and logistical support. Matt Bahm, Kellie Alsup, Lisa Fitzgerald, Micah Zucarelli, John Quinn, Maren Gimple, Shelby Sturgis, Tim Bull, Debbie Morton, Krista Adamek, Jody Bartz, Courtney McCusker, Melissa Hough, Steve Fullington, Audrey DeRose-Wilson, Angie Merritt, and Craig Rekoske provided field assistance. We also thank the landowners in St. Clair and Cedar counties, especially the Bartz, Morton, Seigismund, and Morton families.

LITERATURE CITED

Altwegg, R., T. H. Ringsby, and B. Saether. 2000. Phenotypic correlates and consequences of dispersal in a metapopulation of House Sparrows *Passer domesticus*. Journal of Animal Ecology 69: 762–770.

Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk 115:349–358.

Baker, R. R. 1993. The function of post-fledging exploration: a pilot study of three species of passerines ringed in Britain. Ornis Scandinavica 24:71–79.

Barbraud, C., A. R. Johnson, and G. Bertault. 2003. Phenotypic correlates of post-fledging dispersal in a population of Greater Flamingos: the importance of body condition. Journal of Animal Ecology 72:246–257.

Beardah, C. C. and M. J. Baxter. 1995. MATLAB routines for kernel density estimation and the graphical representation of archaeological data. Anelecta Prehistorica Leidensia 28. Leiden University, Rapenburg, The Netherlands.

Berkeley, L. 2005. The postfledging ecology of Dickcissels (*Spiza americana*). Thesis. University of Nebraska, Omaha, USA.

Cohen, E. B. and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling White-throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. Auk 121:404–414.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43–63.

De Solla, S. R., R. Bonduriansky, and R. J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68:221–234.

Dingemanse, N. J., C. Both, A. J. van Noordwijk, A. L. Rutten, and P. J. Drent. 2003. Natal dispersal and personalities in Great Tits (*Parus major*). Proceedings of the Royal Society of London B 270: 741–747.

Garton, E. O., M. J. Wisdom, F. A. Leban, and B. K. Johnson. 2001. Experimental design for radiotelemetry studies. Pages 16–44 *in* Radio tracking and animal populations (J. J. Millspaugh and J. M. Marzluff, Editors). Academic Press, San Diego, California, USA.

Green, D. J. and A. Cockburn. 2001. Post-fledging care, philopatry, and recruitment in Brown Thornbills. Journal of Animal Ecology 70:505–514.

Greenwood, P. J. and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

Harmeson, J. P. 1974. Breeding ecology of the Dickcissel. Auk 91:348–359.

Helzer, C. J. and D. E. Jelinski. 1999. The relative importance of patch area and perimeter-area ratio

to grassland breeding birds. Ecological Applications 9:1448–1458.

Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecological Applications 4:461–471.

Hooge, P. N. and B. Eichenlaub. 2000. Animal movements extension to ArcView. Version 2.0. USGS, Alaska Science Center, Biological Science Office, Anchorage, USA.

Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. Journal of the American Statistical Association 91:401–407.

Kennedy, P. L. and J. M. Ward. 2003. Effects of experimental food supplementation on movements of juvenile Northern Goshawks (*Accipiter gentilis atricapillus*). Oecologia 134:284–291.

Kenward, R. E., S. S. Walls, and K. H. Hodder. 2001. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. Journal of Animal Ecology 70:1–13.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 126–168 *in* Radio tracking and animal populations (J. J. Millspaugh and J. M. Marzluff, Editors). Academic Press, San Diego, California, USA.

Kershner, E. L., J. W. Walk, and R. E. Warner. 2004. Postfledging movements and survival of juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois. Auk 121:1146–1154.

Lanyon, W. E. 1995. Eastern Meadowlark (*Sturnella magna*). The birds of North America. Number 160.

Magrath, R. D. 1991. Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. Journal of Animal Ecology 60:335–351.

Mathworks. 1999. MATLAB Version 5.3. Natick, Massachusetts, USA.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, USA.

Missouri Climate Center. 2005. Climate bulletin. University of Missouri, Columbia, USA.

Missouri Department of Conservation. 2007. Missouri species and communities of conservation concern. January 2007 checklist. Department of Conservation, Jefferson City, Missouri, USA.

Rappole, J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62: 335–337.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Inigo-Elias, J. A. Kennedy, A. M. Martell, A. O. Panjabi, D. N. Pashley, K. V. Rosenberg, C. W. Rustay, J. S. Wendt, and T. C. Will. 2004. Partners in Flight North American Landbird Conservation Plan. Cornell Laboratory of Ornithology, Ithaca, New York, USA.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American breeding bird survey, results and analysis 1966–2005. Version 2005.2. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.usgs.gov/bbs/bbs.html (accessed 19 February 2007).

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739–747.

SPSS Institute Inc. 1999. SYSTAT. Version 9. SPSS Institute Inc., Chicago, Illinois, USA.

Steel, R. G., J. H. Torrie, and D. A. Dickey. 1997. Principles and procedures of statistics. McGraw-Hill, Boston, Massachusetts, USA.

Suedkamp Wells, K. M. 2005. Resource selection, movement patterns, and survival of post-fledging grassland birds in Missouri. Dissertation. University of Missouri, Columbia, USA.

Suedkamp Wells, K. M., B. E. Washburn, J. J. Millspaugh, M. R. Ryan, and M. W. Hubbard. 2003. Effects of radio-transmitters on fecal glucocorticoid levels in captive Dickcissels. Condor 105:805–810.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100:69–78.

Wand, M. P. and M. C. Jones. 1995. Kernel smoothing. Chapman and Hall, London, United Kingdom.

Wiens, J. D., B. R. Noon, and R. T. Reynolds. 2006. Post-fledging survival of Northern Goshawks: the importance of prey abundance, weather, and dispersal. Ecological Applications 16:406–418.

Winter, M. 1999. Nesting biology of Dickcissels and Henslow's Sparrows in southwestern Missouri prairie fragments. Wilson Bulletin 111:515–527.

Winter, M. and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. Conservation Biology 13:1424–1436.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277–298.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Yackel Adams, A., S. K. Skagen, and R. D. Adams. 2001. Movements and survival of Lark Bunting fledglings. Condor 103:643–647.

Yackel Adams, A., S. K. Skagen, and J. A. Savidge. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87:178–188.

Zimmerman, J. L. 1966. Polygyny in the Dickcissel. Auk 83:534–546.

The Wilson Journal of Ornithology 120(1):131–138, 2008

ECOLOGICAL FACTORS AFFECTING RESPONSE OF DARK-EYED JUNCOS TO PRESCRIBED BURNING

JINELLE H. SPERRY,[1,2,4] T. LUKE GEORGE,[1] AND STEVE ZACK[3]

ABSTRACT.—We compared abundance, daily survival rate, nest site characteristics, food availability, nest activity, and nestling size of Dark-eyed Juncos (*Junco hymenalis*) between burned and unburned mechanically-thinned ponderosa pine (*Pinus ponderosa*) forest units. Dark-eyed Junco territory density, number of detections in point counts, and daily nest survival were similar between treatments. Average bare ground was 4.8 times higher and litter cover was 2.6 times lower at nest sites in burned units compared to unburned nest sites. However, there was 28% less burned area around nests compared to random points in burned units, indicating that juncos placed nests in unburned portions of burned units. They also selected non-traditional nesting sites in burned units such as root holes and in trees. Arthropod abundance was higher in burned units 1-year post burn although numbers were similar in the second-year post burn. Nest attentiveness and feeding rates were three times higher in burned units, possibly in response to increased food availability. The potentially negative effect of prescribed burning through reduction of litter and increase in bare ground was offset by novel nesting strategies and increased food availability. *Received 21 November 2006. Accepted 26 May 2007.*

Traditional management practices, such as logging and fire suppression, have dramatically altered the structure and composition of ponderosa pine (*Pinus ponderosa*) forests in the western United States (Covington and Moore 1994, Veblen et al. 2000). These forests were frequently swept by low-intensity fires, prior to European settlement, that maintained open stands (Covington and Moore 1994, Skinner and Change 1996, Fry and Stephens 2006). Decades of fire suppression have resulted in an accumulation of understory fuels, increased stand density, and encroachment of fire-intolerant species, such as white fir (*Abies concolor*), which can lead to high intensity, stand replacing fires (Covington and Moore 1994). Land managers often use prescribed burning in conjunction with silvicultural thinning to restore ponderosa pine forests to historical conditions and minimize fire risk (Weatherspoon 1996, Covington et al. 1997).

Prescribed burns result in changes in forest structure, soil properties, plant species composition, understory vegetation, ground cover, and arthropod biomass (Rogers 1996, DeLuca and Zouhar 2000, Griffis et al. 2001, Waltz et al. 2003). These changes may positively or negatively affect forest nesting birds by altering habitat structure or food availability. The effects of prescribed burning on birds generally vary with ground and shrub-foraging species typically increasing in abundance following burning (Bock and Lynch 1970, Finch et al. 1997, Bock and Bock 1983, Saab and Powell 2005). Increased abundance of ground-nesting birds following a burn seems unexpected given that burning alters the habitat in ways that should be detrimental.

Our objective was to examine the response of Dark-eyed Juncos (*Junco hyemalis*) to prescribed burning in a mechanically-thinned forest. Specifically, we examined if predicted increase in abundance following prescribed burning results from habitats becoming ecological traps through decreases in ground nest cover or whether behavioral flexibility allows juncos to exploit these habitats successfully.

METHODS

Study Area.—We conducted the study within the Goosenest Adaptive Management Area (GAMA) on the Klamath National Forest in northern California (41° 30 N, 121° 52 W) at an elevation of 1,500 to 1,700 m. The site is

[1] Department of Wildlife, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA.

[2] Current address: Program in Ecology, Evolution and Conservation Biology, University of Illinois Urbana-Champaign, 606 E. Healey, Champaign, IL 61820, USA.

[3] Current address: Wildlife Conservation Society, 718 SW Alder Street, Suite 210, Portland, OR 97205, USA.

[4] Corresponding author; e-mail: jhutch@uiuc.edu

dominated by ponderosa pine, white fir, incense-cedar (*Libocedrus decurrens*), and sugar pine (*Pinus lambertiana*).

The U.S. Forest Service and other cooperators initiated a long-term study in 1996 at GAMA to examine alternative approaches to accelerating late-succession forest characteristics. Five replicates of three silvicultural treatments and a non-treatment "control" were randomly applied to 20 units within GAMA. Each unit was 40 ha and included a 100-m buffer where the silvicultural treatment extended beyond the unit boundary to reduce possible edge effects within the unit. The pine emphasis treatment involved removal of small-diameter trees while retaining large-diameter pines. The pine-emphasis-with-fire treatment involved the same thinning treatment as the pine emphasis units followed by a prescribed burn. Another thinning treatment was applied to five of the units but was not monitored in this study (Ritchie and Harcksen 1999). The most intensive aspects of our study were conducted on the five pine emphasis and five pine-emphasis-with-fire units. We refer to these treatments as unburned and burned treatments, respectively. We also monitored nests on two additional control (unthinned) units although too few juncos were found to include these units in analyses. Thinning treatments started in 1998 and were completed in 2000. The five burned units were prescribed burned in fall 2001. We conducted this study during May–August 2002 and 2003.

Bird Abundance and Nest Survival.—We estimated junco density in each unit using spot mapping and point counts. A 9-ha area (300 × 300 m) in the center of each treatment unit was marked with wire flags every 50 m to assist with spot mapping. Each unit was visited 7–8 times in both 2002 and 2003, and the location, movements, and behavior of all Dark-eyed Juncos were plotted on maps. At the conclusion of the nesting season, territories were delineated and counted following methods described in Bibby et al. (1992). Partial territories were counted if the majority of the territory was within the spot-mapping area.

Point counts were conducted during May and June for both years. Nine points, each 200 m apart, were established within the 9-ha grid area on each unit and each point was surveyed twice by different observers in each year. Point count surveys were started within 15 min of local sunrise and continued until all points on a unit were completed. Count duration was 8 min and started upon arrival at the point. Point counts were not conducted during steady rain, snow, or strong winds (>20 km/hr). All junco detections <100 m from the point were used in analysis. Nest searches were conducted following Martin and Geupel (1993). Nests were monitored every 1–4 days until their fate was ascertained.

Vegetation.—Vegetative characteristics were measured around nest sites and at random grid points in both burned and unburned units. Overstory canopy cover was estimated as the average of four densiometer readings taken 5 m from the site in the four cardinal directions and at the site for a total of 20 readings per site. Shrub cover and woody debris were estimated along two perpendicular 30.8-m transects centered on the nest or random site. Only woody debris with a diameter greater than 7.5 cm and shrubs greater than 0.25 m in height were included.

We also measured vegetative characteristics in a 1-m circle centered on the nest or random site. Litter depth was measured 1 m from the nest or random site in the four cardinal directions. Herbaceous, grass, bare ground, log, and rock cover were visually estimated in a 1-m circle around each nest or random location (Martin et al. 1997). We also estimated the proportion of the area within 1 m of the nest or random site that was burned. Nest concealment directly over the nest cup was visually estimated at every nest where the nest remained intact. All nests, including those in which eggs were not observed, were included in habitat measurements.

Arthropod Sampling.—Arthropod abundance was estimated using pitfall and sticky board traps. Dark-eyed Juncos typically forage on or near the ground (Holmes and Robinson 1988) and our methods targeted ground dwelling or low-flying arthropods. Sticky board traps were made of 30.5 × 30.5 cm corrugated plastic. Each sticky board was covered with a thin layer of Tanglefoot® and placed vertically 4 cm above the ground on metal wires. Following collection, sticky boards were covered in plastic wrap to preserve the samples. Pitfall traps consisted of

TABLE 1. Mean (± SE) number of Dark-eyed Junco territories on 9-ha spot-mapping plots, point count detections, and nesting success of Dark-eyed Juncos on five burned and five unburned units at Goosenest Adaptive Management Area, Klamath National Forest, California, 2002–2003.

Year	Variable	Territories	Detections	Nests (*n*)	Obs. days	Nest success	Daily survival (95% CI)
2002	Burned	5.8 ± 0.6	16.6 ± 3.1	18	207.5	0.29	0.95 (0.92–0.97)
	Unburned	5.0 ± 0.3	17.8 ± 3.8	14	99.5	0.23	0.95 (0.93–0.95)
2003	Burned	2.8 ± 0.7	8.0 ± 0.6	12	191.5	0.41	0.97 (0.96–0.97)
	Unburned	2.8 ± 0.5	7.8 ± 1.1	16	189.5	0.34	0.96 (0.95–0.97)

450-ml containers with holes cut in a circle around the top. Containers were placed with the holes flush to the ground. A lid was placed on the trap to ensure that precipitation and non-target species were excluded. Pitfall traps contained nontoxic propylene glycol as a preservative.

Both trap types were set for two 7-day sampling periods. The first sampling period coincided with Dark-eyed Junco nest building stage (late May 2002, early Jun 2003) and the second coincided with the nestling phase (late Jun 2002, early Jul 2003). Five sticky board and 10 pitfall traps were placed at randomly chosen grid points in each unit. Arthropods were identified to taxonomic order and measured to nearest millimeter. Length-weight ratios were calculated using the general equation in Rogers et al. (1976). Only arthropods 3–20 mm in length were used in the analysis as smaller prey items (<3 mm) and extremely large prey have been shown to be under-represented in the diet of many bird species (Quinney and Ankney 1985, Raley and Anderson 1990, Van Horne and Bader 1990).

Nest Activity.—Digital video cameras were placed at nests for 3 hrs, starting at sunrise, to measure food delivery rates. Nests were videotaped when young were 6 days old and only nests that had four nestlings were used to control for variation in food demands as a function of nestling age and number. We recorded the times when an adult delivered food to the nestlings and the start and end time of each brooding event.

Nestling Measurements.—Wing chord, tarsus, and weight of each nestling in 2003 were measured on the sixth day after hatching. Wing chord and tarsus lengths were recorded with calipers to the nearest 0.5 mm, and weight was measured with an electric balance to the nearest 0.1 g.

Statistical Analysis.—Dark-eyed Junco territory numbers and point count detections were compared between burned and unburned units using two-sample *t*-tests. We used PROC LOGISTIC following Hazler (2004) to analyze daily survival rates (DSR) of nests (SAS Institute 2000). Models were developed using three variables: treatment, mean arthropod biomass by unit, and year. These models were likely to explain variation in daily survival rate of junco nests on our study sites. The candidate set of models was evaluated using Akaike's Information Criteria (Burnham and Anderson 2002) corrected for small sample size (AIC_c). All models were ranked based on relative AIC_c weight (w_i). The model with the lowest ΔAIC_c and highest w_i is considered the best approximating model from the set of candidate models tested (Burnham and Anderson 2002). Actual DSR values were calculated by back transforming logit-scale regression equations. Only nests in which an egg was observed were included in nest survival analysis. Nest/random site characteristics, arthropod biomass, nest activity rates, and nestling measurements were compared between treatments with ANOVAs with unit nested within treatment. Nestling length and weight measurements were averaged for each nest. All ANOVAs and *t*-tests were completed using NCSS (Hintze 2001) statistical program.

RESULTS

Abundance and Nest Survival.—Dark-eyed Junco abundance did not differ significantly between burned and unburned units for either year (Table 1). However, both average number of junco territories and point count detections per unit were higher in 2002 than 2003 (t = 2.23, df = 18, P = 0.04 and t = 3.99, df = 18, P = <0.001, respectively) (Table 1).

Thirty-two nests were monitored in 2002

TABLE 2. Model selection results from Mayfield logistic regression explaining survival of Dark-eyed Junco nests on burned and unburned units at Goosenest Adaptive Management Area, Klamath National Forest, California, 2002–2003. K = number of parameters in each model including the intercept, ΔAIC_c = difference between each model and the model with the lowest AIC_c score, and AIC_c weight = the relative support for each model. Models are ranked based on AIC_c weights.

Model	*K*	ΔAIC_c	AIC_c (wt)	w_i	Rank
Constant survival	1	0	244.24	0.601	1
Arthropod biomass	2	2.45	246.68	0.177	2
Year	2	3.55	247.79	0.101	3
Treatment	2	4.02	248.26	0.081	4
Year + Arthropod	3	6.47	250.71	0.024	5
Year + Treatment	3	7.54	251.78	0.014	6
Year * Treatment	4	11.68	255.91	0.002	7

with 18 nests in burned units and 14 in unburned units. We monitored 28 nests in 2003 with 12 in burned units and 16 on unburned. Daily nest survival was similar between burned and unburned units in both 2002 and 2003 (Table 1). The constant daily survival model received the lowest ΔAIC_c and the greatest AIC_c weight (Table 2).

Nest Activity.—Sample sizes in 2002 were small as few nests survived to day 6 of the nestling period. Four nests in burned and three in unburned units were videotaped. Females spent an average of 35% of their time on the nest in the burned units compared to 12% in the unburned ($F = 8.15$, df = 1, $P = 0.036$). Females spent more time on nests in burned units and we observed more provisioning trips to nests in burned than unburned units (mean ± SE; 0.33 ± 0.06 and 0.11 ± 0.08 trips/min, respectively, $F = 4.27$, df = 1, $P = 0.09$). Sample sizes were also small in 2003 with four nests videotaped in burned and two in unburned units. No differences were detected between burned and unburned units for time spent at nests or number of provisioning trips/min.

Nestling Size.—Mean (±SE) nestling wing chord length on day 6 did not differ between burned and unburned units (21.9 ± 2.02 and 19.5 ± 1.47 mm, respectively; $F = 0.98$, df = 1, $P = 0.25$) nor did mean nestling mass (10.7 ± 0.52 and 9.6 ± 0.67 g, respectively; $F = 1.52$, df = 1, $P = 0.25$).

Nest Site.—Litter depth in 2002 was lower and percent bare ground cover was higher at random sites and around Dark-eyed Junco nests (Table 3) in burned compared to unburned units. Nest concealment did not differ between burned and unburned units (Table 3). There was less burned area around nests than at random locations in burned units (23.8 and 51.7%, respectively; $F = 4.09$, df = 1, $P =$

TABLE 3. Mean (± SE) values of habitat variables at random sites on burned and unburned units at Goosenest Adaptive Management Area, Klamath National Forest, California, 2002–2003.

Year	Variable	Random burned	Random unburned	*P*	Nest burned	Nest unburned	*P*
2002	Woody debris, %	0.86 ± 0.45	2.58 ± 0.44	0.14	0.82 ± 0.56	2.53 ± 0.56	0.068
	Shrub cover, %	1.15 ± 2.33	6.12 ± 2.29	0.21	3.01 ± 2.83	8.10 ± 2.83	0.36
	Litter depth, cm	0.52 ± 0.32	2.75 ± 0.31	0.001	0.89 ± 0.40	2.35 ± 0.40	0.038
	Bare ground, %	49.27 ± 4.72	24.01 ± 4.62	0.005	35.59 ± 6.31	7.35 ± 3.27	0.002
	Nest concealment, %				80.0 ± 6.23	87.79 ± 3.63	0.33
	n	25	25		17	17	
2003	Woody debris, %	1.27 ± 0.85	4.88 ± 0.85	0.052	2.29 ± 1.06	6.24 ± 1.03	0.090
	Shrub cover, %	2.82 ± 1.28	5.35 ± 1.28	0.37	3.32 ± 1.66	6.35 ± 1.51	0.35
	Litter depth, cm	1.29 ± 0.46	2.51 ± 0.41	0.037	1.96 ± 0.46	3.26 ± 0.41	0.066
	Bare ground, %	36.8 ± 4.10	24.00 ± 4.10	0.058	20.62 ± 4.66	20.00 ± 7.61	0.95
	Nest cover, %				86.64 ± 5.44	82.87 ± 4.66	0.61
	n	25	25		15	18	

TABLE 4. Mean (± SE) values of arthropod biomass (g) on burned and unburned units at early and late sampling dates at Goosenest Adaptive Management Area, Klamath National Forest, California, 2002–2003. Arthropod biomass was estimated using general length-weight ratios (Rogers et al. 1976).

Year	Trap type	Season	Burned	Unburned
2002	Sticky board	Early	40.39 ± 2.16	22.27 ± 2.68
	Sticky board	Late	28.33 ± 2.31	20.97 ± 2.68
	Pitfall	Early	24.84 ± 3.62	35.80 ± 4.02
	Pitfall	Late	22.64 ± 3.44	21.14 ± 3.90
2003	Sticky board	Early	16.22 ± 1.05	15.54 ± 1.14
	Sticky board	Late	9.53 ± 1.40	13.04 ± 1.51
	Pitfall	Early	19.74 ± 2.67	20.66 ± 3.00
	Pitfall	Late	20.65 ± 3.34	27.02 ± 2.75

0.048). Percent bare ground in 2003 was higher, litter depth was lower, and there was less woody debris at random sites in burned compared to unburned units (Table 3). None of the nest site variables differed between burned and unburned units and none differed between nest and random sites on either treatment in 2003 (Table 3).

Two severe wind events during winter 2002–2003 caused extensive windfall on the study units. There were more fallen trees in 2003 around nest sites than at random sites in both the burned (mean ± SE; 3.07 ± 0.65 and 1.52 ± 0.50, respectively; $F = 5.51$, df = 1, $P = 0.026$) and unburned units (3.3 ± 0.59 and 1.6 ± 0.50, respectively; $F = 3.41$, df = 1, $P = 0.074$).

Arthropod Abundance.—Coleopterans and dipterans accounted for most arthropods caught on sticky board traps. Both treatment (burned vs. unburned) and sampling periods differed in 2002 (Tables 4, 5) while only sampling period differed in 2003 (Table 5). Mean biomass was higher in burned units compared to unburned and higher in May compared to June (Table 4). Most arthropods caught in pitfall traps in both burned and unburned units were Hymenoptera (ants) and Diptera. Mean arthropod biomass in pitfall traps did not differ between treatments, sampling period or year (Tables 4, 5).

DISCUSSION

Several studies have documented increases in abundance of ground-nesting birds following prescribed burning (Bock and Lynch 1970, Bock and Bock 1983, Saab and Powell 2005). We found Dark-eyed Juncos were equally abundant in burned and unburned units suggesting that response of ground-nesting birds to prescribed fire is variable. Responses may depend on a variety of factors including the nesting and foraging ecology of the bird species, size of the burn, burn severity, and time since burn (Finch et al. 1997).

Daily nest survival did not differ between

TABLE 5. Effects of treatment (burned and unburned, df = 1), unit (df = 8), sampling date (df = 1) and interactions from nested ANOVA on biomass of arthropods in sticky board and pitfall traps at Goosenest Adaptive Management Area, Klamath National Forest, California, 2002–2003. Arthropod biomass was estimated using general length-weight ratios (Rogers et al. 1976).

	Treatment		Date		Unit		Treatment × Date		Unit × Date	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
2002										
Sticky board	13.61	0.006	7.34	0.045	4.75	0.061	1.98	0.045	1.01	0.43
Pitfall	0.49	0.50	5.04	0.055	2.75	0.14	1.88	0.058	0.58	0.80
2003										
Sticky board	0.36	0.57	12.73	0.007	2.66	0.14	2.77	0.005	0.81	0.59
Pitfall	2.60	0.15	1.52	0.25	0.85	0.38	1.28	0.25	2.18	0.026

treatments (burned vs. unburned), year, or as a function of arthropod biomass. Juncos achieved equal nesting success in burned and unburned units indicating they were able to overcome the effects of reduced nesting cover. Burned habitats did not function as ecological traps and our results were broadly consistent with the behavioral flexibility hypothesis.

Nest concealment is a major factor affecting nest success of passerines and an important aspect of nest-site selection (Martin and Roper 1988, Howlett and Stutchbury 1996, Flaspohler et al. 2000, Weidinger 2002). We expected that nest concealment would be substantially lower on burned than unburned units but we found no difference between treatments. Similarity in nest concealment, despite a decline in suitable cover in burned units, can be explained by two nesting strategies used by juncos. First, juncos often placed their nests in unburned patches in burned units as ground cover on the burned units did not burn uniformly, which is common for both prescribed burns and wild fires in this forest type (Weatherspoon 1996). Second, juncos used non-traditional nesting sites. Two nests were on mats of pine needle >10 m high in trees and many nests were found under overhanging rocks or in burned root holes. Juncos were not observed nesting in these types of sites in unburned units or in burned units prior to burning. These results suggest that nest concealment was an important nest site criterion for juncos on our study area.

A large wind throw event during winter 2002–2003 provided abundant down wood on all units in 2003, further reducing the difference between burned and unburned units. Dark-eyed Juncos used this increased ground structure by placing their nests in areas of greater wind throw compared to random sites, regardless of treatment.

We documented an overall increase in low-flying arthropod biomass, particularly dipterans and coleopterans, in burned units in the spring following the prescribed burn. Biomass of ground arthropods in pitfall traps was similar between burned and unburned units. These results are broadly consistent with previous studies that demonstrated that wood and bark boring beetles increased following fire to exploit weakened trees (McCullough et al. 1998, Santoro et al. 2000) while ground arthropods generally declined due to decreased litter, altered soil properties, and direct fire mortality (McCullough et al. 1998, Wikars and Schimmel 2001, Dress and Boerner 2004). Many arthropods associated with ground or shrub foliage, such as homopterans and Lepidoptera larvae, were not present in large numbers at our study site due to reduction in vegetation caused by thinning treatments and prescribed burns. All arthropod Orders known to be used as prey by juncos increased in burned units 1 year after burning suggesting there may have been more food available.

Analysis of junco nest activity demonstrated that adults spent more time on the nest in burned than in unburned units. Provisioning rates were also greater in burned units, possibly due to higher nest visitation rates by the non-brooding adult. Higher arthropod abundance in burned units may have influenced nest attentiveness and provisioning rates.

Dark-eyed Juncos demonstrated flexibility in nest placement in areas that were prescribed burned. By using novel nesting strategies, juncos were able to find suitable nesting cover. The behavioral plasticity displayed by Dark-eyed Juncos seems likely to be an evolved response that has allowed them to exploit recurring changes in habitat. The positive response to prescribed burning documented in other ground-nesting bird species may be a product of similar behavioral plasticity.

ACKNOWLEDGMENTS

We are grateful to W. W. Oliver, M. W. Ritchie, and Bill Reynolds of the Pacific Southwest Research Station, USDA Forest Service in Redding, California and the Goosenest Ranger District for funding and support. We thank Michael Verbit, Jarred Wolfe, Donna Germann, Katisha Jasper, Alex Powell, and Emily Campbell for assistance in the field and with insect identification. We also thank M. D. Johnson, M. A. Camann, D. M. Sperry, J. D. Brawn, P. J. Weatherhead, M. J. Willis, and an anonymous reviewer for helpful comments and suggestions on earlier versions of this manuscript.

LITERATURE CITED

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird census techniques. Academic Press, London, United Kingdom.

Bock, C. E. and J. H. Bock. 1983. Responses of birds and deer mice to prescribed burning in ponderosa

pine. Journal of Wildlife Management 47:836–840.

Bock, C. E. and J. F. Lynch. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72:182–189.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, USA.

Covington, W. W. and M. M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. Journal of Forestry 92: 39–47.

Covington, W. W., P. Z. Fule, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. Journal of Forestry 95:39–47.

DeLuca, T. H. and K. L. Zouhar. 2000. Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. Forest Ecology and Management 138:263–271.

Dress, W. J. and R. E. Boerner. 2004. Patterns of microarthropod abundance in oak-hickory forest ecosystems in relation to prescribed fire and landscape position. Pedobiologia 48:1–8.

Finch, D. M., J. L. Ganey, Y. Wang, R. T. Kimball, and R. Sallabanks. 1997. Effects and interactions of fire, logging, and grazing. Pages 103–136 *in* Songbird ecology in southwestern ponderosa pine forests: a literature review (W. M. Block and D. M. Finch, Technical Editors). General Technical Report RM-292. USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Flaspohler, D. J., S. A. Temple, and R. Rosenfield. 2000. The relationship between nest success and concealment in two ground-nesting passerines. Journal of Field Ornithology 71:736–747.

Fry, D. L. and S. L. Stephens. 2006. Influence of humans and climate on the fire history of a ponderosa pine-mixed conifer forest in the southeastern Klamath Mountains, California. Forest Ecology and Management 223:428–438.

Griffis, K. L., J. A. Crawford, M. R. Wagner, and W. M. Moir. 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. Forest Ecology and Management 146:239–245.

Hazler, K. R. 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. Auk 121:707–716.

Hintze, J. 2001. NCSS and PASS. Number Cruncher Statistical Systems, Kaysville, Utah, USA.

Holmes, R. T. and S. K. Robinson. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. Wilson Bulletin 100:377–394.

Howlett, J. S. and B. J. Stutchbury. 1996. Nest concealment and predation in Hooded Warblers: experimental removal of nest cover. Auk 113:1–9.

Martin, T. E. and G. R. Geupel. 1993. Nest-monitoring units: methods for locating nests and monitoring success. Journal of Field Ornithology 64: 507–519.

Martin, T. E. and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.

McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and arthropods in northern and boreal forest ecosystems of North America. Annual Review of Entomology 43:107–127.

Quinney, T. E. and C. D. Ankney. 1985. Prey size selection by Tree Swallows. Auk 102:245–250.

Raley, C. M. and S. H. Anderson. 1990. Availability and use of arthropod food resources by Wilson's Warblers and Lincoln's Sparrows in southeastern Wyoming. Condor 92:141–150.

Ritchie, M. W. and K. A. Harcksen. 1999. Long-term interdisciplinary research on the Goosenest Adaptive Management Area, Klamath National Forest, California. Forestry Chronicle 75:453–456.

Rogers, L. E., W. T. Hinds, and R. L. Buschbom. 1976. A general weight vs. length relationship for arthropods. Annals of the Entomological Society of America 69:387–389.

Rogers, P. 1996. Disturbance ecology and forest management: a review of the literature. General Technical Report INT-GTR-336. USDA, Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Saab, V. A. and H. D. Powell. 2005. Fire and avian ecology in North America: process influencing pattern. Studies in Avian Biology 30:1–13.

Santoro, A. E., M. J. Lombardero, M. P. Ayers, and J. J. Ruel. 2000. Interactions between fire and bark beetles in an old growth pine forest. Forest Ecology and Management 144:245–254.

SAS Institute. 2000. SAS/STAT software: changes and enhancements. Release 8.1. SAS Institute, Cary, North Carolina, USA.

Skinner, C. N. and C. R. Change. 1996. Fire regimes, past and present. Sierra Nevada Ecosystem Project: final report to Congress. Volume 2. Assessments and scientific basis for management options. University of California, Davis, USA.

Van Horne, B. and A. Bader. 1990. Diet of nestling Winter Wrens in relationship to food availability. Condor 92:413–420.

Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecological Applications 10:1178–1195.

Waltz, A. E., P. Z. Fulé, W. W. Covington, and M. M. Moore. 2003. Diversity in ponderosa pine forest structure following ecological restoration treatments. Forest Science 49:885–900.

WEATHERSPOON, C. P. 1996. Fire-silviculture relationships in Sierra forests. Sierra Nevada Ecosystem Project: final report to Congress. Volume 2. Chapter 44. Centers for Water and Wildland Resources, University of California, Davis, USA.

WEIDINGER, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424–437.

WIKARS, L. AND J. SCHIMMEL. 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. Forest Ecology and Management 141:189–200.

The Wilson Journal of Ornithology 120(1):139–145, 2008

WINTER HABITAT USE BY BOREAL CHICKADEE FLOCKS IN A MANAGED FOREST

ADAM HADLEY[1] AND ANDRÉ DESROCHERS[1,2]

ABSTRACT.—There are increasing conservation concerns associated with boreal regions, but little is known about winter habitat requirements of bird species inhabiting them. We examined flock size, winter habitat preference, and home range size of Boreal Chickadees (*Poecile hudsonica*) in a boreal forest harvested for timber near Quebec City, Quebec, Canada. We investigated whether and to what extent home range size was affected by clearcuts and regeneration forest stands. Flocks included an average of four individuals and occupied a mean winter home range of 14.7 ha. Flock membership and size were stable during the winter. Boreal Chickadees strongly preferred mature stands of commercial value (>7 m in height) and used regenerating stands (4–7 m in height) to a lesser extent. Younger stands (<4 m in height) and open areas were avoided. Home range size was not associated with landscape composition, but flocks with larger home ranges used them less evenly than those with smaller home ranges. This resident species prefers stands of commercial value and logging may contribute to apparent population declines of Boreal Chickadees. *Received 23 September 2006. Accepted 31 March 2007.*

Logging is considered the most important threat to birds inhabiting boreal forest regions (Imbeau et al. 2001) and is rapidly modifying North America's boreal forests. Approximately 300,000 ha of boreal forest in Quebec, Canada have been clearcut annually in recent years (Ministère des Ressources naturelles et de la Faune 2006). This logging practice is leading to a dramatic regional reduction in large tracts of mature forest and a subsequent increase in younger successional stages. The remaining forest patches are typically restricted to riparian buffer strips and buffers between adjacent clearcuts (Ministère des Ressources naturelles 1996).

Among birds, resident species are hypothesized to be most exposed to loss and fragmentation of boreal forests (Imbeau et al. 2001, Schmiegelow and Mönkkönen 2002). Population dynamics of resident species inhabiting northern latitudes appear to be strongly affected by events occurring during the non-breeding season (Matthysen 1990, Lahti et al. 1998, Doherty and Grubb 2002). Many resident species inhabiting boreal forests in Europe have undergone marked population declines hypothesized to result from forest harvesting (Imbeau et al. 2001). Despite increasing conservation concerns associated with boreal regions, little is known about winter habitat requirements of bird species inhabiting them.

The Boreal Chickadee (*Poecile hudsonica*) is a boreal forest resident which exemplifies the lack of knowledge of wintering birds within these regions. The Breeding Bird Survey, despite its weak sampling effort for boreal species, reports an alarming decline of Boreal Chickadees (mean annual change 1966–2004 = −3.59%, $P = 0.0035$) in eastern North America (Sauer et al. 2005). This species is listed as highly vulnerable to changes induced by modern forestry (Imbeau et al. 2001). The Boreal Chickadee is often considered the North American ecological equivalent of the Grey-headed Chickadee (*P. cincta*); a species that has also undergone dramatic declines due to the effects of forestry practices (Imbeau et al. 2001).

Flocks of Boreal Chickadees form as soon as young fledge and persist throughout the non-breeding season (Sep–late Apr) (Ficken et al. 1996). Winter survival is thought to set population limits for Boreal Chickadees (Erskine 1977, 1992) and concern has been expressed about suitability of the remaining habitat in winter (Erskine 1992, Foss 1994, Cyr and Larivée 1995). Increasing the proportion of non-habitat and sub-optimal habitat within a landscape can increase the size of an animal's home range (Gjerde and Wegge 1989, Storch 1993, Siffczyk et al. 2003). However, winter home range characteristics and habitat use, despite their obvious implications for management, are virtually unknown for this species (Ficken et al. 1996).

[1] Centre d'étude de la forêt, Faculté de foresterie et de géomatique, Université Laval, Québec, Québec, G1K 7P4, Canada.

[2] Corresponding author; e-mail: andre.desrochers@sbflulaval.ca

Our objective was to measure the relative occurrence of Boreal Chickadees in mature and regenerating forest stands in a region managed for timber and recreational use. We tested whether flock size and interspecific composition were stable during winter months. We also tested whether size of Boreal Chickadee home ranges was associated with the area of clearcuts and regenerating stands. We predicted that flocks with large home ranges would occur predominantly in certain parts of their ranges (Carr and Macdonald 1986) and flocks with smaller home ranges would distribute their activities more evenly throughout their home range.

METHODS

Study Area.—We collected data during winters 2004–2005 and 2005–2006 at the Forêt Montmorency, Quebec, Canada (47° 20′ N, 71° 10′ W). The study area is a 66 km² boreal forest mosaic managed for timber exploitation and recreational use. Mature coniferous stands (>7 m in height) cover ~56% of the study area. Balsam fir (*Abies balsamea*) and occasionally black spruce (*Picea mariana*) dominate mature stands, interspersed with white birch (*Betula papyrifera*). Younger seral stages (4–7 m in height) were characterized by sapling balsam fir, black spruce and, to a lesser extent, mixed regeneration. These cover 24% of the study area. Open areas consisting of clearcuts, lakes, rivers, roads >7 m in width, and sapling stands <4 m in height cover 20% of the study area. An extensive road network (2.6 km/km²) crosses the research forest.

Use of Forest Stands.—We investigated habitat use from 85 unmarked Boreal Chickadee flocks. Seventy-two flocks were studied in the first winter (6 Jan–10 Mar 2004) and 13 flocks during the following winter (14 Feb–24 Mar 2005). We combined data from both years since no major differences in weather or food availability were observed. We located chickadee flocks each day using randomly selected points on a systematic 1-km spaced grid covering the study area. Grid points were visited only once during the study and we located flocks by snowshoeing a systematic search pattern. We started from the selected grid point and moved 500 m north, 500 m east, 1,000 m south, 500 m west, and 500 m north to return to the point of origin. All flock detections were passive (no use of playback or "pishing"). Flocks members were unmarked and we assumed that a new flock was monitored each day, as flock composition differed in all but three cases of adjacent flocks (known to be separate due to simultaneous observations). We followed flocks on snowshoes and plotted their locations in real time at 1-min intervals using a hand held Trimble™ GPS receiver (PDOP < 8). One-minute sampling intervals were used because serial correlation is irrelevant when using the proportion of an animal's trajectory contained within each habitat type for compositional analysis (Aebischer et al. 1993). Frequent sampling more closely approximates the underlying trajectory and provides a more precise estimate of proportional habitat use (Aebischer et al. 1993, Barg et al. 2005). No positions were recorded during the first 2.5 min following discovery of a flock. We followed each flock for as long as possible not exceeding 3 hrs. Positions were recorded only when we were at the approximate center of the flock; data recording ceased immediately if observer position no longer represented that of the flock. The following period for a flock was also terminated if the observer lost contact. We then moved to another grid sampling point before recommencing the search for different flocks. The time we followed flocks ranged from 5 to 152 min (mean = 53 min) and path lengths ranged from 90 to 2,125 m (mean = 871 m). The total distance traveled following 85 flocks was 74 km in 75 hrs. We observed no discovery bias since there was no relationship ($R^2 = 0.001$, $F = 3.4$, $P = 0.06$) between stand type and time elapsed since initial discovery of a flock.

We divided the habitat within the study area into three categories: (1) mature forest (stand >7 m in height), (2) regeneration (4–7 m in height), and (3) open areas (stands <4 m in height or areas devoid of vegetation above snow). Stand seral stages were characterized using existing GIS coverage for the study area (validated *in situ*, delimited by GPS, and mapped with ArcView 3.3 [ESRI 2002]). We established a measure of available habitat representative of home range size (Jones 2001) by delineating a 200-m buffer surrounding the movement path for each flock. We generated

a 10-m spaced grid of points within each buffer. The resulting grid points were assumed to represent unbiased samples of the habitat due to the apparent lack of spatial periodicity in the stand types of the study area. We used compositional analysis (Aebischer et al. 1993) to examine if used habitat (observed locations) differed from available habitat within 200 m (grid points). We replaced missing values in log ratios (available but not used) with 0.001, at least one order of magnitude less than the smallest non-zero value for that habitat type, as suggested by Aebischer et al. (1993). We used SAS (SAS Institute Inc. 2004) and BYCOMP.SAS macro (Ott and Hovey 1997) to compute the randomization procedure recommended by Aebischer et al. (1993). Only flocks having all three habitat types represented within the "available habitat" were used in the analysis. This constraint reduced the sample size to 79 flocks.

Home Range Estimation.—We calculated home range sizes using data collected from color-marked flocks of Boreal Chickadees during winter 2004–2005. Twenty-three members of seven flocks were captured from 6 December 2004 to 3 February 2005 using mist nets and playbacks of chickadees mobbing a stuffed owl. We marked birds with USGS numbered aluminum bands and unique color combinations. We fitted color bands with ~1 cm long flags of colored electrician's tape to enhance visibility for up to 10 m without use of binoculars (Desrochers et al. 1988).

Each marked flock received seven visits between 7 February and 24 March 2005. We randomized the order and time of visits among marked flocks, and successive visits were separated by 2–7 days. We located marked flocks using short (5 sec) bursts of Boreal Chickadee calls on a portable speaker audible to 70 m and by searching on snowshoes in concentric circles around the initial capture locations. Bursts of playback were short and restricted in frequency to limit effects on flock movements. We ceased playbacks if answering calls were heard and proceeded directly to where the birds were located. We identified flocks by band combinations and flock composition was recorded at the beginning of each visit. We followed flocks during each visit using the same procedure as with unmarked flocks. The time that we followed marked flocks during each visit ranged from 5 to 165 min (mean = 43 min). We recorded successive locations when they were separated by at least 5-min intervals. Points were considered biologically independent as chickadees could easily move to any point within their home range during this time period (Barg et al. 2005). The number of locations per flock ranged from 48 to 83 (mean ± SE = 69 ± 5 points).

We calculated home range size using both the minimum convex polygon (MCP) and 95% kernel methods. The MCP was used to allow comparison with other studies of parids (Harris et al. 1990). However, the MCP allows little insight into internal configuration of used spaces, is highly affected by peripheral locations, and can contain larger areas not used by the organism (Harris et al. 1990, Barg et al. 2005). We addressed these shortcomings by using a fixed kernel density estimator to study the density distribution of observations and to construct each flock's distribution of use (UD). We used the 95% fixed kernel to define the kernel home range size and the 50% fixed kernel area (containing 50% of the observations) to define the core area for each flock. Fixed kernel density estimations were performed using the Animal Movement extension in ArcView 3.3 (Hooge and Eichenlaub 1997). We used least squares cross validation (LSCV) for each flock to calculate the optimal smoothing parameter. Least squares cross validation provides the least biased estimates for smoothing parameters (Worton 1995, Seaman and Powell 1996).

Correlates of Home Range Size.—We compiled the proportion of different stand seral stages within MCP and kernel home ranges, and examined their association with home range sizes. We also calculated a variable (USE) representing the distribution of locations within the home range. USE was obtained by calculating the difference between the 95% and 50% (CORE) kernel estimations (Siffczyk et al. 2003). The USE variable provided information on whether flock locations were concentrated in distinct areas of the home range (high USE values) or evenly distributed throughout the home range (low USE values). Flocks with home ranges containing patchy, widely distributed, resources would be expected to have large USE values (concentrates use in select locations) and larger home

TABLE 1. Relationships among home range size, landscape composition, flock size, and use patterns within home ranges of seven marked Boreal Chickadee flocks. Correlation coefficients are shown with *P*-values in parentheses (Spearman rank correlation). Home range size = 100% minimum convex polygon (ha); USE = difference between the 95% and 50% kernels (ha). Habitat proportions represent proportions within MCP.

Variable	Home range size
Proportion of mature stands in home range	−0.57 (0.2)
Proportion of regeneration stands in home range	0.14 (0.8)
Proportion of open area in home range	0.39 (0.4)
Flock size	0.26 (0.6)
USE	0.89 (0.007)

range sizes. Flocks with evenly distributed resources would be expected to have lower USE values (more even use of home range) and smaller home ranges.

The association between landscape components and home range size was examined using Spearman rank correlations (SAS Institute Inc. 2004). Effects were considered significant at $\alpha = 0.05$.

RESULTS

Use of Forest Stands.—Boreal Chickadee flocks did not use mature forest, regenerating forest, and open areas at random (Wilks' Lambda = 0.22, $F = 134$, $P < 0.001$, $n = 79$). Mature forest was used more frequently than regenerating forest (mean log-ratio = 7.16, $P < 0.001$) or open areas (mean log-ratio = 16.44, $P < 0.001$), and regenerating forest was used more frequently than open areas (mean log-ratio = 3.60, $P < 0.001$).

Flock and Home Range Size.—We used data from all 85 flocks of Boreal Chickadees and found that mean (±SE) flock size was 4 ± 0.2 with a range of three to eight Boreal Chickadees. Sixteen of 85 flocks contained at least one Black-capped Chickadee (*Poecile atricapillus*) (4 ± 0.4, range = 1–10 within these 16 flocks) and Red-breasted Nuthatches (*Sitta canadensis*) were present in 27 of 85 flocks (4 ± 0.3, range = 2–8 within these 27 flocks). Nine flocks contained all three species. Black-capped Chickadees appeared to form cohesive flocks with Boreal Chickadees and remained in close contact with Boreal Chickadees throughout the entire following period. Red-breasted Nuthatches were associated with Boreal Chickadees only as loose foraging groups (they followed at a distance, often leaving and rejoining flocks). We used seven flocks of marked individuals to learn that flock membership and size remained stable throughout winter months (Jan–Mar). We observed no apparent immigration, emigration, or mortality over a 6-week period in the seven marked flocks. No banded individuals disappeared or moved between flocks and the total number of individuals within flocks remained unchanged.

Boreal Chickadee flocks occupied a mean (± SE) home range size of 14.7 ± 3.2 ha (MCP, $n = 7$) with a range of 7.9 to 30.4 ha. Mean home range size using the 95% fixed kernel was actually larger, 16.9 ± 3.4 ha (95% kernel, $n = 7$) with a range of 7.6 to 33.9 ha. Flocks had a mean (± SE) core area of 2.3 ± 0.7 ha (50% kernel, $n = 7$) with a range of 1.0 to 5.8 ha.

Landscape Structure and Home Range Size.—Boreal Chickadee MCP home ranges contained 61 ± 9% mature forest (range = 21–94%), 23 ± 10% regeneration forest (range = 0–79%), and 15 ± 6% open area (range = 0–43%). We found no relationship between landscape components and MCP home range size (Table 1). However, we believe the trend of increasing MCP home range size with increasing proportion of open area (Fig. 1A) and decreasing home range size with increasing proportion of mature forest (Fig. 1B) has biological significance. Flocks with larger home ranges concentrated use in several distinct areas (large differences between 95% and 50% core areas) while flocks with smaller home ranges used their home range more evenly (Table 1). Home range size was not associated with flock size (Table 1).

DISCUSSION

Boreal Chickadee flocks are similar to wintering flocks of other northern parid species in size and member stability. Mean flock size (4

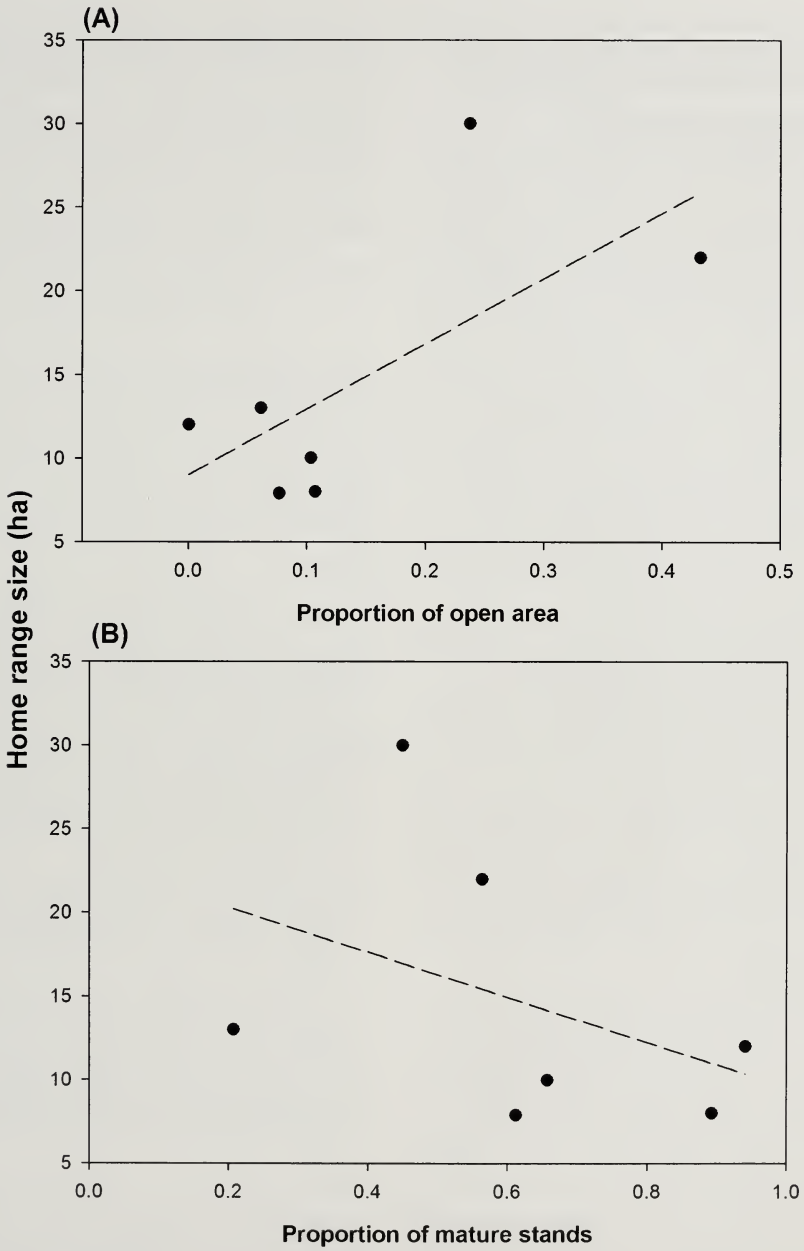


FIG. 1. Association between MCP home range size and (A) proportion of open area within home ranges, and (B) proportion of mature stands within home ranges of Boreal Chickadees, Quebec, Canada, 2004–2005. Trend lines are not significant.

± 0.2 individuals) was slightly larger than Grey-headed Chickadee winter flocks, which average between two and three individuals (Virkkala 1990). Willow tits (*Poecile montana*) form, on average, four-bird flocks (Ekman 1989, Siffczyk et al. 2003), while Black-capped Chickadees usually form slightly larger flocks with six to eight individuals (Smith 1991). Our marked flocks showed member stability throughout the winter, as is thought to be the case with most parids (Desrochers and Hannon 1989, Ekman 1989). Boreal

Chickadees formed mixed species flocks similar to many wintering parids (Hogstad 1987, Smith 1991), but most often maintained flocks solely composed of conspecifics.

Boreal Chickadee flocks preferred mature forest stands and avoided young successional stages or open areas (Fig. 1, Table 1). Mature forest stands were strongly preferred to regeneration stands, but flocks frequently spent time in regenerating forest habitat. Boreal Chickadee flocks rarely spent time in open areas (when lone trees were available or when crossing gaps). These results are consistent with information on breeding habitat use by Boreal Chickadees. Whitaker and Montevecchi (1997) considered the Boreal Chickadee to be a forest generalist within coniferous wooded areas. Erskine (1977) also showed Boreal Chickadees used both mature and young forest during the breeding season.

Our flocks had winter home range sizes of 14.7 ha, comparable to those of Black-capped Chickadees (9.5–14.6 ha [Smith 1991]; 22.4 ha [Desrochers and Fortin 2000]) and Willow Tits (12.6 ha [Siffczyk et al. 2003]) during the non-breeding season. Sizes of winter home ranges were not significantly associated with forest composition. However, our flocks had similar tendencies of increasing home range size with inclusion of a larger proportion of non-habitat to those demonstrated previously (Gjerde and Wegge 1989, Storch 1993, Siffczyk et al. 2003).

Differences in space use patterns depending on the size of winter home range likely reflect the patchiness of resources within large home ranges. Flocks with large home ranges focused their activity in distinct locations within their home range while flocks with smaller home ranges distributed their activities more evenly across space. These results agree with the resource dispersion hypothesis (RDH), which predicts that home ranges will be large when patches of resources are widely spaced (Carr and Macdonald 1986). Similar results have been shown for Willow Tits (Siffczyk et al. 2003).

Boreal forests in eastern North America are being subjected to intensive forest exploitation (Ministère des Ressources naturelles et de la Faune 2006). Extensive logging has resulted in a reduction in the proportion of mature forest with a subsequent increase in proportion of young forest or open areas (Imbeau et al. 1999, Ministère des Ressources naturelles et de la Faune 2006). Consequently, forestry practices will result in substantial reduction of optimal Boreal Chickadee wintering habitat, at least over several decades. Our findings are consistent with the hypothesis that apparent population declines in this species result from loss of high-quality wintering habitat.

ACKNOWLEDGMENTS

We thank David Duchesne, Marc Lamarre, and Geneviève d'Anjou for help in the field. We are grateful to the staff at Forêt Montmorency (Université Laval) for logistical support. M. G. Betts, Louis Imbeau, S. G. Cumming, and M. S. Hadley provided useful comments on the manuscript. This study was funded by a NSERC Discovery grant to André Desrochers and a NSERC Postgraduate scholarship (PGS A) to A. S. Hadley.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313–1325.

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

Carr, G. M. and D. W. Macdonald. 1986. The sociality of solitary foragers - a model based on resource dispersion. Animal Behaviour 34:1540–1549.

Cyr, A. and J. Larivée. 1995. Atlas saisonnier des oiseaux du Québec. Presses de l'Université de Sherbrooke et Société de loisir ornithologique de l'Estrie, Sherbrooke, Québec, Canada.

Desrochers, A. and M.-J. Fortin. 2000. Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. Oikos 91:376–384.

Desrochers, A. and S. J. Hannon. 1989. Site-related dominance and spacing among winter flocks of Black-capped Chickadees. Condor 91:317–323.

Desrochers, A., S. J. Hannon, and K. E. Nordin. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. Auk 105:727–736.

Doherty Jr., P. F. and T. C. Grubb Jr. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83:844–857.

Ekman, J. 1989. Ecology of non-breeding social systems of *Parus*. Wilson Bulletin 101:263–288.

Erskine, A. J. 1977. Birds in boreal Canada: communications, densities, and adaptations. Canadian Wildlife Service Report Series 41. Canadian Wildlife Service, Ottawa, Ontario, Canada.

Erskine, A. J. 1992. Atlas of breeding birds of the Maritime Provinces. Nimbus Publications and Nova Scotia Museum, Halifax, Nova Scotia, Canada.

ESRI. 2002. ArcView® 3.3 GIS. Environmental Systems Research Institute Inc., Redlands, California, USA.

Ficken, M. S., M. A. McLaren, and J. P. Hailman. 1996. Boreal Chickadee. The birds of North America. Number 254.

Foss, C. R. (Editor). 1994. Atlas of breeding birds in New Hampshire. Audubon Society, Dover, New Hampshire, USA.

Gjerde, I. and P. Wegge. 1989. Spacing pattern, habitat use and survival of Capercaillie in a fragmented winter habitat. Ornis Scandinavica 20: 219–225.

Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20:97–123.

Hogstad, O. 1987. Social rank in winter flocks of Willow Tits *Parus montanus*. Ibis 129:1–9.

Hooge, P. N. and B. Eichenlaub. 1997. Animal movement extension to ArcView. Version 2.0. USGS, Alaska Science Center, Anchorage, USA.

Imbeau, L., M. Mönkkönen, and A. Desrochers. 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. Conservation Biology 15: 1151–1162.

Imbeau, L., J.-P. L. Savard, and R. Gagnon. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. Canadian Journal of Zoology 77:1850–1860.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557–562.

Lahti, K., M. Orell, S. Rytkonen, and K. Koivula. 1998. Time and food dependence in Willow Tit winter survival. Ecology 79:2904–2916.

Matthysen, E. 1990. Nonbreeding social organization in *Parus*. Current Ornithology 7:209–249.

Ministère des Ressources naturelles. 1996. Règlement sur les normes d'intervention dans les forêts du domaine public. Gazette Officielle du Québec 128:2750–2786.

Ministère des Ressources naturelles et de la Faune. 2006. Ressources et industries forestières : portrait statistique. Gouvernement du Québec, Québec City, Canada.

Ott, P. and F. Hovey. 1997. BYCOMP.SAS. Clearinghouse for ecology software. Available at: http://nhsbig.inhs.uiuc.edu/wes/habitat.html.

SAS Institute Inc. 2004. SAS software. Version 9.1. SAS Institute Inc., Cary, North Carolina, USA.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American breeding bird survey, results and analysis 1966–2004. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schmiegelow, F. K. A. and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecological Applications 12:375–389.

Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Siffczyk, C., L. Brotons, K. Kangas, and M. Orell. 2003. Home range size of Willow Tits: a response to winter habitat loss. Oecologia 136:635–642.

Smith, S. M. 1991. The Black-capped Chickadee: behavioral ecology and natural history. Cornell University Press, Ithaca, New York, USA.

Storch, I. 1993. Patterns and strategies of winter habitat selection in alpine Capercaillie. Ecography 16: 351–359.

Virkkala, R. 1990. Flock size of the Siberian Tit *Parus cinctus* during the non-breeding season. Ornis Fennica 67:98–99.

Whitaker, D. M. and W. A. Montevecchi. 1997. Breeding bird assemblages associated with riparian, interior forest, and nonriparian edge habitats in a balsam fir ecosystem. Canadian Journal of Forest Research 27:1159–1167.

Worton, B. J. 1995. Using Monte-Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.

The Wilson Journal of Ornithology 120(1):146–152, 2008

LONG-TERM EFFECTS OF WASTEWATER IRRIGATION ON HABITAT AND A BIRD COMMUNITY IN CENTRAL PENNSYLVANIA

ADAM T. ROHNKE[1,3] AND RICHARD H. YAHNER[2,4]

ABSTRACT.—We studied the possible long-term (1987 vs. 2003–2004) effects of wastewater irrigation of forests to habitat and a songbird community in central Pennsylvania. The study site, Toftrees, is a wastewater-irrigated deciduous forest interspersed with agriculture grasslands and crop fields that receives ~260 cm of wastewater annually. Habitat variables were quantified within 15 random 0.04-ha circular plots in 2003 and 20 random plots in 1987. We conducted bird surveys twice weekly during 2003 and mist-netted birds for 1,250 hrs during 2004. Surveys and mist-netting efforts paralleled those conducted in 1987. A major decline in density of understory trees and short shrubs was noted between 1987 and 2003; in contrast, cover of herbaceous vegetation and density of tall shrubs dramatically increased. Ground-shrub foraging bird species and two mid-canopy foragers, Red-eyed Vireo (*Vireo olivaceus*) and Eastern Wood-Pewee (*Contopus virens*), declined from 1987 to 2003–2004. Conversely, Gray Catbirds (*Dumetella carolinensis*) increased dramatically over this time period. *Received 18 November 2005. Accepted 27 April 2007.*

Long-term trends in a bird community may be affected by many environmental factors, including habitat alteration, pollutants, invasive species, and exotic pathogens (Gill 1995, Rohnke 2005). Habitat alteration can have dramatic effects on food supply, nesting sites, cover, and other habitat features for native birds (Johnston 1970); bird density and diversity are related to vegetative structure of forests (MacArthur and MacArthur 1961, Johnston 1970, Dickson and Noble 1978).

Sewage treatment and wastewater disposal impact to watersheds and associated habitats has been a major concern of municipalities across the United States (Kelso and Bowersox 2004). A growing number of municipalities (22 in 1985) have initiated land application of wastewater since the Federal Water Pollution Act of 1970 as an alternative to discharging treated wastewater directly into rivers and lakes (Rollfinke 1988). Several studies of waste water irrigated forests have documented effects including changes in structure and species composition of the overstory, understory, mid-canopy, and the forest floor (Cole et al. 1986, Kelso and Bowersox 2004). These changes are attributed to modification of soil moisture chemistry, and tree and shrub loss as a result of significant ice buildup during below freezing periods in winter (Cole et al. 1986, Rollfinke 1988, Kelso and Bowersox 2004).

The Pennsylvania State University began irrigating wastewater experimentally onto forests, fields, and farmland at the Toftrees site in 1963 and expanded to the current facility in 1983 (Kelso and Bowersox 2004). Five years post expansion, Rollfinke (1988) documented limited change in species composition and density of the overstory, understory, and herbaceous vegetation in the irrigated forest. Rollfinke (1988) concluded that small modifications to the winter irrigation schedule should alleviate much of the stress placed upon the forests. For example, limiting irrigation to days with temperature above freezing or irrigating crop fields and open areas that are exposed to sun instead of shaded forested areas would reduce breakage of understory tree limbs from ice. A comprehensive vegetation study by Kelso and Bowersox (2004) noted moderate change in species composition of the overstory trees and substantial change in the species composition of sapling and seedling layers in the irrigated forest. In addition, herbaceous plants and non-native shrubs dominated the forest floor and understory of the irrigated community. Kelso and Bowersox (2004) concluded the current man-

[1] School of Forest Resources, 111 Ferguson Building, The Pennsylvania State University, University Park, PA 16802, USA.

[2] School of Forest Resources, 119 Forestry Resources Building, The Pennsylvania State University, University Park, PA 16802, USA.

[3] Current address: Central Mississippi Research and Extension Center, 1320 Seven Springs Road, Raymond, MS 39154, USA.

[4] Corresponding author; e-mail: rhy@psu.edu

agement regime would not be able to sustain a forest community because of reduced regeneration and selective pressure towards non-native shrub species in the irrigated forest.

Pre-expansion studies by Savidge and Davis (1971) and Greenwald (1981) documented limited changes to the local bird communities at Toftrees prior to facility expansion. Rollfinke and Yahner (1990) reported an increase in species richness in 1988 (5 years post-expansion), but diversity declined because the bird community became dominated by several forest edge species (i.e., Common Yellowthroat [*Geothlypis trichas*], Indigo Bunting [*Passerina cyanea*], and Song Sparrow [*Melospiza melodia*]). Rollfinke and Yahner (1990) specifically noted that wastewater irrigation may be detrimental to Wood Thrush (*Hylocichla mustelina*) and other ground-nesting and ground-dwelling bird species. They concluded wastewater irrigation had limited effect generally on the bird community at Toftrees. However, Rollfinke and Yahner (1990) cautioned that effects of wastewater irrigation would continue to affect the structure of the forest (i.e., ice damage, limited regeneration of saplings, and dense herbaceous plant cover) and encouraged long-term studies to document gradual effects of wastewater irrigation on the forest bird communities at Toftrees. The objective of our study was to examine long-term (1987 vs. 2003–2004) effects of wastewater irrigation on habitats and a songbird community at a wastewater irrigation site in central Pennsylvania.

METHODS

Study Area.—The Toftrees area is a 209-ha wastewater irrigated site in Centre County, Pennsylvania (40° 50′ 15″ N, 77° 53′ 50″ W). Overstory trees (≥1.5 m tall, ≥7.5 cm dbh) are primarily oak (*Quercus* spp.) and red maple (*Acer rubrum*), interspersed with aspen (*Populus* spp.) and pine (*Pinus* spp.) (Rollfinke 1988, Rohnke 2005). Major understory trees (≥1.5 m tall, 2.5–7.5 cm dbh) and shrubs (0.5–1.00 m tall, <2.5 cm diameter) include red maple, white ash (*Fraxinus americana*), tartarian honeysuckle (*Lonicera tatarica*), rose (*Rosa* spp.) (Rhoads and Klein 1993), dogwood (*Cornus* spp.), and wild grape (*Vitis* spp.). Additionally, old fields and limited active agriculture fields are present. Agriculture areas were not included in either of the surveys.

The wastewater irrigation system comprised 3,100 rotating sprinkler heads connected by a network of surface and buried lateral pipelines (Rollfinke and Yahner 1990). Approximately 260 cm of wastewater are applied annually (Rollfinke and Yahner 1990, Kelso and Bowersox 2004) with wastewater more than doubling the average annual rainfall of 103 cm (National Climatic Data Center, The Pennsylvania State University). Several areas (each 0.01 ha or smaller) of standing water and permanent ponds have formed since installation of the spray system in April 1983 (Rollfinke 1988).

Habitat Sampling.—We quantified the same habitat variables within 15 random 0.04-ha circular sampling plots during summer 2003 that Rollfinke (1988) quantified in 20 plots in 1987. Habitat variables quantified within plots included densities (number/ha) of overstory live trees and snags (stems ≥1.5 m tall, >7.5 cm dbh), stumps (<1.5 m tall, >7.5 cm diameter), and logs (≥1 m length, >7.5 cm diameter) (modified from James and Shugart 1970). Habitat variables measured within two perpendicular transects (1 × 10 m) inside the sampling plots included densities (number/ha) of understory trees (woody stems ≥1.5 m tall, 2.5–7.5 cm dbh), tall shrubs (woody stems ≥1.5 m tall, <2.5 cm diameter), and short shrubs (stems >1.5 m tall, <2.5 cm diameter); only stems rooted within the area of the perpendicular transects were counted. Multi-stemmed species were counted as individual stems if a stem was unbranched and singularly emerged from the soil. Percent canopy cover, herbaceous ground cover, and leaf litter were recorded at 20 ocular tube readings at 2-m intervals along the perpendicular transects, giving 10 readings/transect. Average vegetation height (cm) was measured along each perpendicular transect and once in the center of the 0.04-ha plot in field habitats only.

We calculated means (± SE) of habitat variables from all plots combined. Means for each variable were compared between 1987 (Rollfinke 1988) and 2003 by percent change over this time period.

Transect Surveys of Birds.—We established four transects, each 200 to 400 m in length, (at least 104 m apart) with a combined length

of 1,000 m per site. A proportional sample of available habitats (i.e., field [30%], early successional [35%], and mature forests [35%]) totaling 10 ha (1,000 × 100 m) was surveyed. We counted all birds heard or seen within a 50-m lateral distance of transects while walking ~1.6 km/hr (Conner and Dickson 1980). Birds flying over or through the forest canopy were not recorded. We did not conduct surveys during heavy precipitation or when winds exceeded 20 km/hr. Surveys were conducted twice weekly, June–August 2003 (n = 18), at each site from sunrise to 1100 hrs EDT to replicate sampling effort by Rollfinke (1988).

Mean species richness (± SE), total number of contacts (number/10 ha) for all species combined, and number of contacts for individual species (number/10 ha) were calculated for 1987 (Rollfinke 1988) and at Toftrees in 2003. Raw data from 1987 at Toftrees were not available for statistical comparison and we calculated percent change in means between 1987 and 2003.

Mist-netting of Birds.—We mist-netted birds from June through October 2004. Mist nets (n = 6–8) were placed between 10 and 50 m apart along the same transects used for bird surveys. We sampled birds at mist nets along each transect for 2 consecutive days; mist nets were generally in operation from 0.5 hr before sunrise to 1400 hrs each sampling day. Nets were closed because of precipitation, high wind velocity (≥20 km/hr), or heat from direct sunlight to minimize levels of avian stress and possible mortality (Rohnke 2005). We opened nets during ~250 hrs per transect, giving 1,250 total net hrs/year, as in 1987 (Rollfinke 1988). Nets were rotated and moved no more than 10 m from the center of the original net lanes (2 × 12 m plot cleared of all above-ground vegetation for placement of mist nets) during the season to increase capture success and reduce net avoidance (Rollfinke 1988). We fitted all captured birds with a single numbered federal aluminum band for identification purposes (Pyle et al. 1997) and recorded age, gender, mass (g), and wing and tarsus length (mm) (Rollfinke 1988). Birds previously captured during the season were recorded as recaptures and measured again.

We used breeding 'safe' dates to ascertain whether captured individuals were breeding residents or migrants in central Pennsylvania. Safe dates calculated by the Pennsylvania Breeding Bird Atlas are conservative (1 Jun–31 Jul; Robert Mulvihll and Mike Lanzone, pers. comm.). We used a more liberal range of dates because we were interested in not only recording breeding resident birds but also hatch-year and nonbreeding birds during summer.

Our 'adjusted safe dates' were 15 May–6 August and were based on Pennsylvania Breeding Bird Atlas safe dates and banding records at both sites. All birds captured within the adjusted safe dates were considered resident and those captured outside of the adjusted safe dates (not previously banded) were migrants. Chi-square goodness-of-fit tests (Sokal and Rohlf 1995) were used to compare total individuals captured of each species between 1987 and 2004.

RESULTS

Habitat Sampling.—Overstory and understory tree density decreased by 69 and 49%, respectively, in 2003 versus 1987 (Table 1). Density of tall shrubs increased (447%) in 2003 compared to 1987, whereas densities of short shrubs decreased by 80% in 2003 versus 1987. Densities of logs decreased 58% and densities of stumps decreased 96% in 2003 compared with 1987. Canopy cover decreased (28%) but herbaceous ground cover and leaf litter increased (21 and 92%, respectively) from 1987 compared with 2003.

Transect Sampling of Birds.—Mean total contacts of all species combined and mean species richness increased by 89 and 16%, respectively, from 1987 to 2003 (Table 2). We noted 43 species in 2003 compared with 34 in 1987. Major increases (change >50%) in number of contacts of 15 species were noted in 2003 compared with 1987. Of these 15 species, we noted dramatic increases (change >1,000%) in three species including American Robin (*Turdus migratorius*), Gray Catbird (*Dumetella carolinensis*), and Song Sparrow. Major decreases (change >−50%) were observed in number of contacts of nine species, including Hairy Woodpecker (*Picoides villosus*), Pileated Woodpecker (*Dryocopus pileatus*), Eastern Wood-Pewee (*Contopus virens*), Great Crested Flycatcher (*Myiarchus crini-*

TABLE 1. Habitat variables (means ± SE) measured at 0.04-ha circular plots in 1987 (n = 20) and 2003 (n = 15) at Toftrees, Centre County, Pennsylvania. Data from 1987 are from Rollfinke (1998).

Variable	Year		% change
	1987	2003	
Overstory tree, all species, (number/ha)	708 ± 42	217 ± 49	−69
Understory tree, all species, (number/ha)	669 ± 101	336 ± 157	−49
Tall shrub, all species, (number/ha)	1,447 ± 304	7,909 ± 2,126	+447
Short shrub, all species, (number/ha)	6,645 ± 902	1,330 ± 4,725	−80
Physical features, (number/ha)			
Logs	305 ± 34	127 ± 30	−58
Stumps	68 ± 17	3 ± 2.3	−96
Percent cover			
Canopy	72 ± 3.8	52 ± 7.7	−28
Herbaceous ground cover	57 ± 3.8	69 ± 6.7	+21
Leaf litter	14 ± 3.0	27 ± 7.0	+92

TABLE 2. Mean number of contacts (± SE) per species (number/10 ha), mean total contacts (all species combined), mean species richness, and total species observed along 1,000 m of transects (10 ha) at Toftrees, Centre County, Pennsylvania, during 1987 (Rollfinke 1988) and 2003. Only those 29 species observed in both years and only species with changes > ±50% are shown. Percent change was calculated between years.

Species	Toftrees		
	1987	2003	% change
Mourning Dove[a] (*Zenaida macroura*)	0.06 ± 0.06	0.56 ± 0.18	826
Red-bellied Woodpecker[a] (*Melanerpes carolinus*)	0.06 ± 0.06	0.22 ± 0.13	270
Hairy Woodpecker[b]	1.00 ± 0.24	0.33 ± 0.16	−67
Pileated Woodpecker[b]	0.28 ± 0.14	0.11 ± 0.08	−61
Eastern Wood-Pewee[b]	1.06 ± 0.22	0.11 ± 0.08	−90
Great Crested Flycatcher[b]	0.89 ± 0.29	0.39 ± 0.18	−56
Red-Eyed Vireo[b]	8.00 ± 0.59	2.22 ± 0.39	−72
Blue Jay[a] (*Cyanocitta cristata*)	0.61 ± 0.33	1.94 ± 0.36	219
American Crow[a]	0.22 ± 0.10	1.83 ± 0.51	733
Wood Thrush[b]	3.28 ± 0.64	1.56 ± 0.28	−53
American Robin[c]	0.44 ± 0.18	8.11 ± 1.43	1,743
Gray Catbird[c]	0.11 ± 0.08	12.33 ± 1.30	11,112
Cedar Waxwing[a]	0.28 ± 0.16	2.89 ± 0.54	932
American Redstart[a]	1.39 ± 0.23	4.61 ± 0.77	232
Ovenbird[b]	0.33 ± 0.12	0.06 ± 0.06	−83
Common Yellowthroat[a]	4.50 ± 0.35	10.50 ± 1.00	133
Northern Cardinal[a]	1.22 ± 0.31	3.00 ± 0.50	146
Rose-Breasted Grosbeak[a]	0.17 ± 0.09	1.78 ± 0.44	946
Indigo Bunting[b]	3.89 ± 0.28	1.89 ± 0.45	−51
Eastern Towhee[b]	3.89 ± 0.43	1.11 ± 0.24	−71
Song Sparrow[c]	0.17 ± 0.09	12.89 ± 0.99	7,482
Brown-Headed Cowbird[a] (*Molothrus ater*)	1.17 ± 0.35	2.50 ± 0.71	114
Common Grackle[a] (*Quiscalus quiscula*)	0.44 ± 0.17	0.94 ± 0.46	115
American Goldfinch[a]	0.33 ± 0.14	2.44 ± 0.50	641
Mean total contacts[a]	44.60 ± 2.12	84.17 ± 4.28	89
Mean species richness	17.50 ± 0.57	20.33 ± 0.65	16

[a] Percent change > 50.
[b] Percent change > −50.
[c] Percent change > 1,000.

TABLE 3. Total individuals mist-netted (recaptures not included) per species at Toftrees, Centre County, Pennsylvania during 1987 (Rollfinke 1988) and 2004. Only the 23 species with >10 contacts and captured in both years are shown. Data were based on ~ 1,250 hrs of mist net operation during each year. Goodness-of-fit tests were performed on common (observed ≥20 captures) species.

Species	Toftrees	
	1987	2004
Downy Woodpecker (*Picoides pubescens*)	9	1
Black-Capped Chickadee (*Poecile attricapillus*)	9	5
American Robin	5	10
Gray Catbird[a]	60	115
American Redstart	12	8
Ovenbird	7	3
Common Yellowthroat	23	15
Eastern Towhee	11	7
Song Sparrow[a]	116	54
Northern Cardinal	13	9
Indigo Bunting[a]	34	7
American Goldfinch[a]	21	3
Total individuals[a]	320	237

[a] $\chi^2 > 10.83$, df = 1, $P < 0.001$.

tus), Wood Thrush, Red-eyed Vireo (*Vireo olivaceus*), Ovenbird (*Seiurus aurocapillus*), Eastern Towhee (*Pipilo erythrophthalmus*), and Indigo Bunting.

Mist-netting of Birds.—We mist-netted 280 individual birds representing 31 species in 2004 (Table 3). The six most common species included American Robin, Gray Catbird, American Redstart (*Setophaga ruticilla*), Common Yellowthroat, Song Sparrow, and Northern Cardinal (*Cardinalis cardinalis*). Rollfinke (1988) mist-netted 384 individuals representing 36 species at Toftrees in 1987 with the five most common being Gray Catbird, Common Yellowthroat, Song Sparrow, Indigo Bunting, and American Goldfinch (*Carduelis tristis*).

Only the Gray Catbird increased ($P < 0.001$) from 1987 to 2004 (Table 3). We documented declines ($P < 0.001$) for Indigo Bunting, Song Sparrow, and American Goldfinch. Song Sparrows were the second most abundant bird species in 2004. Total number of individuals ($P < 0.001$) mist-netted declined in 2004 versus 1987.

DISCUSSION

Habitat Variables.—Year-round wastewater irrigation affected the vegetation at Toftrees as predicted by Greenwald (1981) and documented by Rollfinke et al. (1990). Overstory trees were affected by winter ice damage and routine selective logging to remove safety hazards (Cole et al. 1986, Kelso and Bowersox 2004). Tall and short shrubs densities also were impacted by ice buildup from year-round irrigation on the site (Cole et al. 1986, Rollfinke et al. 1990). The primary causes for the increase in herbaceous vegetation height and density were likely increases in soil moisture and nutrient concentrations (e.g., nitrogen) (Mastrota et al. 1989). Changes in species and density at the Toftrees site were likely the result of secondary succession.

Our observation of declining densities of overstory and understory trees at Toftrees since 1987 may be problematic because of minimal regeneration in the understory of tree saplings established after 1983, which was the year of installation of the wastewater irrigation system (Kelso and Bowersox 2004). The overstory canopy at Toftrees may be reduced more over time if this lack of regeneration continues, which will further alter vegetation structure and corresponding bird communities. Tall shrubs increased between 1987 and 2003 at Toftrees; consistent with findings of Kelso and Bowersox (2004), but their tall shrub density was not as high as in our study. The Kelso and Bowersox (2004) study used similar methods and their sampling included several of our study plots but also several plots in different areas of the Toftrees site.

We found that most tall shrubs were tartar-

ian honeysuckle and rose, which are invasive, exotic shrub species that thrive in disturbed ecosystems (Rhoads and Klein 1993). Seed bank and sapling studies by Kelso and Bowersox (2004) documented that wastewater irrigation had strong negative effects on presence of native tree and shrub species. They concluded a variety of factors could be limiting the establishment of native shrub and tree seedlings including overstory and understory competition, browse pressure, and seed sources being mostly comprised of upland species.

We noted that percent cover of leaf litter nearly doubled at Toftrees between 1987 and 2003 although Rollfinke (1988) concluded that high soil moisture accelerated decomposition of leaf litter. The increase of tall shrub density was likely attributed partially to an increase in foliage, resulting in greater amounts of leaf litter.

Avian Community.—The Indigo Bunting, compared with 1987 (Rollfinke 1988), dramatically decreased in 2003–2004; this species has declined slightly on a regional scale (Sauer et al. 2005). We have no biological explanation for the large decline in numbers of this species, except perhaps perching and singing sites have been reduced as a result of fewer overstory and understory trees.

Total contacts combined and mean species richness increased in 2003–2004; consistent with findings by Rollfinke and Yahner (1990). Major declines in understory vegetation presumably impacted some ground-shrub and mid-canopy foragers, as indicated by a decline in species richness and total individuals during mist-netting in 2004. Rollfinke and Yahner (1990) also reported population declines in Wood Thrush and Ovenbird since the onset of wastewater irrigation in 1983. We detected a decline in Eastern Towhee in 2004, which parallels a steady decline of this species over the past two decades in the northeastern United States (Hagan 1993, Sauer et al. 2005). The Song Sparrow, another declining species on our study site, decreased on a regional scale but is considered common in Pennsylvania (McWilliams and Brauning 2000, Sauer et al. 2005).

Greenwald (1981) predicted that canopy species, including Eastern Wood-Pewee and Red-eyed Vireo, should be found in similar abundance in both pre- and post-irrigation eras at Toftrees. Our study documented a decrease in populations of both species based on transect surveys in 2003 compared to 1987. Decreases of overstory trees on the study area may partially account for the lower density of these species on a local scale. Regionally, the Eastern Wood-Pewee has steadily declined since 1966, whereas the Red-eyed Vireo has increased steadily since 1966 (Sauer et al. 2005).

The "park-like understory," as described by Kelso and Bowersox (2004) in wooded stands at Toftrees provides habitat for several edge species to expand into the forest interior (Rollfinke and Yahner 1990). For example, American Crow (*Corvus brachyrhynchos*), American Robin, American Redstart, Common Yellowthroat, and American Goldfinch increased in the forest interior between 1987 and 2004. Frugivores (e.g., Cedar Waxwing [*Bombycilla cedrorum*], Gray Catbird, and Rose-Breasted Grosbeak [*Pheucticus ludovicianus*]) may have benefited from the dramatic increase in tartarian honeysuckle on the site; these species are primary dispersal agents of its seeds (Nickell 1965).

Long-term trends in the local bird community indicated that local habitat alteration in response to wastewater irrigation have affected some species. Kelso and Bowersox (2004) concluded that natural processes cannot sustain a forest community under the current management plan at Toftrees. The avian community will lose forest dependent bird species (canopy and mid-canopy) over time as a result of the change in vegetation structure and will be mostly comprised of secondary successional bird species (i.e., Gray Catbird, Song Sparrow, Common Yellowthroat, etc.). We predict continuing declines in ground nesting species, including Wood Thrush and Ovenbird. These changes will result in a decline in mean bird species richness over time.

ACKNOWLEGMENTS

We thank K. C. Kim and G. J. San Julian, and referees for comments on earlier drafts. We thank M. C. Brittingham, R. R. Charnick, D. M. Cramer, J. T. Demarco, M. R. Marshall, M. F. McDermott, P. M. McElhon, and B. D. Ross for logistical and field assistance. E. H. Hill assisted with preparation of the manuscript. This study was funded by the Pennsylvania Agricultural Experiment Station and the Office of

Physical Plant and Wastewater Operations at The Pennsylvania State University.

LITERATURE CITED

Cole, D. W., C. H. Henry, and W. L. Nutter (Editors). 1986. The forest alternative for treatment and utilization of municipal and industrial wastes. University of Washington Press, Seattle, USA.

Conner, R. N. and J. G. Dickson. 1980. Strip transect sampling and analysis for avian habitat studies. Wildlife Society Bulletin 8:4–10.

Dickson, J. G. and R. E. Noble. 1978. Vertical distribution of birds in a Louisiana bottomland hardwood forest. Wilson Bulletin 90:19–30.

Gill, F. B. 1995. Ornithology. Second Edition. W. H. Freeman and Company, New York, USA.

Greenwald, C. M. 1981. Prediction of songbird responses to habitat alteration resulting from wastewater irrigation. Thesis. Pennsylvania State University, University Park, USA.

Hagan, J. M. 1993. Decline of the Rufous-sided Towhee in the eastern United States. Auk 110:863–874.

James, F. and H. H. Shugart Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Johnston, D. W. 1970. High density of birds breeding in a modified deciduous forest. Wilson Bulletin 79–82.

Kelso, L. M. and T. W. Bowersox. 2004. Long-term effects of wastewater irrigation on forested ecosystems in central Pennsylvania. Journal of the Pennsylvania Academy of Science 78:43–52.

MacArthur, R. H. and J. W. MacArthur. 1961. On species diversity. Ecology 42:494–498.

Mastrota, F. N., R. H. Yahner, and G. L. Storm. 1989. Small mammal communities in a mixed-oak forest irrigated with wastewater. American Midland Naturalist 122:388–393.

McWilliams, G. M. and D. W. Brauning. 2000. The birds of Pennsylvania. Cornell University Press, Ithaca, New York, USA.

Nickell, W. P. 1965. Habitats, territory, and nesting of the Catbird. American Midland Naturalist 73:433–478.

Pyle, P., S. N. G. Howell, D. F. DeSante, R. P. Yunick, and M. Gustafson. 1997. Identification guide to North American birds. Volume 1. Slate Creek Press, Bolinas, California, USA.

Rhoads, A. F. and W. M. Klein. 1993. The vascular flora of Pennsylvania: annnotated check-list and atlas. Proceedings of the American Philosophical Society, Philadelphia, Pennsylvania, USA.

Rohnke, A. T. 2005. Possible ecological effects of habitat alteration and West Nile virus on songbird populations in central Pennsylvania. Thesis. Pennsylvania State University, University Park, USA.

Rollfinke, B. F. 1988. Avian communities in wastewater-irrigated deciduous forests in central Pennsylvania. Thesis. Pennsylvania State University, University Park, USA.

Rollfinke, B. F. and R. H. Yahner. 1990. Community structure and composition of breeding and wintering birds in a wastewater-irrigated oak forest. Journal of Wildlife Management 54:493–500.

Rollfinke, B. F., R. H. Yahner, and J. S. Wakeley. 1990. Effects of forest irrigation on long-term population trends in breeding-bird communities. Wilson Bulletin 102:264–278.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, results and analysis 1996–2004. Version 2005.2. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.gov/bbs/bbs.html (accessed 28 May 2005).

Savidge, I. R. and D. E. Davis. 1971. Bird populations in an irrigated woodlot 1963–1967. Bird Banding 42:249–263.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry. Third Edition. W. H. Freeman and Company, New York, USA.

The Wilson Journal of Ornithology 120(1):153–158, 2008

LONG-TERM TRENDS IN BREEDING BIRDS IN AN OLD-GROWTH ADIRONDACK FOREST AND THE SURROUNDING REGION

STACY A. McNULTY,[1,3] SAM DROEGE,[2] AND RAYMOND D. MASTERS[1]

ABSTRACT.—Breeding bird populations were sampled between 1954 and 1963, and 1990 and 2000 in an old-growth forest, the Natural Area of Huntington Wildlife Forest (HWF), in the Adirondack Mountains of New York. Trends were compared with data from regional North American Breeding Bird Surveys (BBS) and from a forest plot at Hubbard Brook Experimental Forest, New Hampshire. Trends for 22 species in the HWF Natural Area were negative, eight were positive, and one was zero; 20 were significant. Fifteen of 17 long-distance migrants declined, whereas 7 of 14 short-distance migrants and permanent residents declined. Most (74%) HWF Natural Area species, despite differences in sampling periods and local habitat features, matched in sign of trend when compared to Adirondack BBS routes, 61% matched northeastern BBS routes, and 71% matched eastern United States BBS routes, while 66% matched Hubbard Brook species. The agreement in population trends suggests that forest interior birds, especially long-distance migrants, are affected more by regional than local factors. The analysis indicated that bird trends generated from BBS routes may not be as biased toward roads as previously suggested. *Received 14 February 2007. Accepted 22 June 2007.*

Avian trend data at both local and regional scales are important for setting conservation priorities, and documenting patterns of decline, increase, and stability (Robbins et al. 1989, Faaborg 2002). Long-term monitoring of land-bird populations is uncommon because sustaining monitoring programs longer than a few years is difficult. As an example, forest birds in North America were not widely surveyed until ~40 years ago, and data from only a handful of sites surveyed prior to the 1960s (or sites comparable to them) have continued to be available (cf. Holmes and Sherry 2001). Studies of longer duration are of immeasurable value in documenting change and potential conservation needs for breeding bird species, especially because variances in estimates tend to be high (Thompson and Schwalbach 1995).

The primary source of long-term information on trends in populations of breeding landbirds in North America is the Breeding Bird Survey (BBS) (Peterjohn 1994). This survey, initiated in 1966, is both temporally and spatially extensive, and is based on permanent survey points along randomly selected secondary roads (blocked by latitude and longitude) throughout the United States and southern Canada. Publication of trends resulting from BBS data led to programs in the late 1980s to survey forest interiors in selected parts of the continent (Cadman et al. 1998, Faccio et al. 1998) to corroborate or complement large scale BBS trends from roadside counts.

The BBS is affected by a number of known biases that influence estimates of population trends (Link and Sauer 1998). One area of potential bias in BBS data is placement of survey points along roadways. The results may be biased toward trends that reflect human-disturbed habitat which may be disproportionately represented along roads (O'Connor 1989). Hagan et al. (1997) found that estimated population trends of landbirds in Maine did not correlate well with BBS results, likely because local habitat (industrial forest) differed from that around survey routes.

The objectives of this paper are to: (1) compare bird population trends from data collected in 1954–1963 and 1990–2000 in an old growth tract in the central Adirondacks to trends based on BBS data from the region and to trends in a forest plot at Hubbard Brook Experimental Forest, New Hampshire, and (2) evaluate whether local trends match those at range-wide scales, a finding that would indicate the need to shift bird conservation priorities toward regional rather than local scales.

METHODS

Study Area.—Our sampling points were in the Natural Area on Huntington Wildlife Forest (HWF), a 6,000-ha research station in the central Adirondack Mountains. HWF is operated by

[1] Adirondack Ecological Center, SUNY Environmental Science and Forestry, 6312 Route 28N, Newcomb, NY 12852, USA.

[2] USGS, Patuxent Wildlife Research Center, BARC-EAST, Building 308, Room 124, 10300 Baltimore Avenue, Beltsville, MD 20705, USA.

[3] Corresponding author; e-mail: smcnulty@esf.edu

the Adirondack Ecological Center of the State University of New York, College of Environmental Science and Forestry (44° 0′ 26.3″ N, 74° 16′ 12.4″ W, 488–579 m elevation) in the towns of Newcomb, Essex County, and Long Lake, Hamilton County, New York, USA. The HWF Natural Area is 365 ha of predominantly northern hardwood forest dominated by American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*), interspersed with eastern hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*). The age of many trees in the HWF Natural Area is 200–300 years: tree age was measured by increment boring. The shrub layer consists mainly of witch hobble (*Viburnum lantanoides*) and beech, with ground cover consisting of ferns (mostly *Dryopteris spinulosa*) and forbs. The study portion of the HWF Natural Area is >2.75 km from the nearest road and is most likely primary or old-growth forest (Leopold et al. 1988; Adirondack Ecological Center, unpubl. data).

No catastrophic events drastically altered the habitat during the years of the surveys. However, old-growth forests are subject to processes that alter the vegetative composition over time. For example, a wind storm in 1950 created several canopy openings in the stand that were largely closed by 1954, the first year of the original study (Webb et al. 1977). Other long term changes in vegetation structure and floristics have been documented. Timber inventories of the study area in 1948 and 1993 indicated that number of trees >9.14 cm diameter at breast height (dbh) decreased from 74.2 to 65.4/ha (Adirondack Ecological Center, unpubl. data). The number of sugar maple stems in this same size class declined from 20.2 to 10.5% of the stand, red spruce declined from 18.7 to 3%, and beech increased from 39.7 to 68.8%. Overall, conifers declined from 28.2 to 5.2% with most declines in the 9.14–29.46 cm diameter class. Basal area of all trees decreased from 32.62 to 26.56 m^2/ha with the greatest changes occurring in trees >29.46 cm dbh where basal area declined from 23.35 to 18.07 m^2/ha. The understory component of the stand (trees 1.5–9.14 cm, dbh) increased in stem density from 122.2 to 166.3/ha. This increase was driven by mortality of beech >30 cm dbh due primarily to beech bark disease which resulted in extensive root sprouting (Jones and Raynal 1987).

Sampling Methodology.—Six bird survey points spaced 0.27 km apart in a 1 × 6 grid were established in 1954 in the HWF Natural Area to serve as a control for a study of the effects of logging on songbirds (Webb et al. 1977). Surveys were conducted in June from 1954 to 1963 by a combination of five observers and all points were visited an average 2.4 times per year (range 1–4). RDM sampled these points from 1990 to 2000 in the same manner for an average of 3.6 surveys (range 2–5) each year.

Survey observers recorded all birds heard or seen without regard for distance for 10 min at each point. Surveys were conducted on calm, non-rainy mornings from dawn until noon. Data recorded after 0800 hrs EST were not included in this analysis to minimize the impact of decreased species detection in the later morning hours (Webb et al. 1977). Chimney Swifts (*Chaetura pelagica*) were excluded as it was unclear whether this aerial feeder was consistently counted across years.

Statistical Analyses.—Trends in counts were calculated for the HWF Natural Area using Poisson regression (Hedeker and Gibbons 1994) with date of survey as a co-variable (the BBS website calculator was not used). Significance level was set at *alpha* = 0.05. English and scientific bird names follow the most recent AOU checklist (AOU 1998). We defined long-distance (or neotropical) migrants as species that winter largely outside of North America, short-distance migrants as species that winter largely in the southern United States, and permanent residents as species that remain in breeding areas year-round.

We obtained estimates of bird population trends for 1966–2000 from the BBS (Sauer et al. 2001) for the following regions: Adirondack Mountains (n = 25 routes); northeastern United States (ME, NH, VT, RI, MA, CT, NJ, NY, PA, MD, WV, and VA) (n = 623 routes); and all eastern North American physiographic regions (n = 1,710 routes) (Sauer et al. 2001). Each BBS survey includes 50, 3-min counts taken at points spaced 0.8 km apart, conducted once each spring. Trends were calculated using the estimating equation route regression method (Link and Sauer 1998).

Estimates of population trends for north-

eastern forest birds for 1969–1998 were obtained from one 10-ha breeding bird census plot established in the Hubbard Brook Experimental Forest, New Hampshire (Holmes and Sherry 2001). This census plot is within a large contiguous tract of secondary northern hardwood forest resulting from selective logging in the early 1900s. The forest is dominated by sugar maple, American beech, and yellow birch with scattered red spruce. Population trends were calculated using linear regression models for abundance over time.

RESULTS

Trends at the HWF Natural Area.—We had sufficient data from the HWF Natural Area for trend analysis of 31 species: the trends were negative for 22, positive for eight, and one showed no change (Table 1). Thirteen of 22 negative trends (59%) were significant, whereas seven (88%) positive trends were significant. Fifteen of 17 long-distance migrants declined, one increased, and one did not change; 12 of 15 negative estimates were significant. Seven of 12 short-distance migrants were declining (3 significantly) and five were increasing (all significantly). One of two resident species, Black-capped Chickadee (*Poecile atricapillus*), declined nonsignificantly while Hairy Woodpecker (*Picoides villosus*) increased significantly. Only American Redstarts (*Setophaga ruticilla*) and Winter Wrens (*Troglodytes troglodytes*) had a significantly declining trend with sampling date. The number of birds not identified to species was tracked across all years and no significant trend was detected.

The most precipitously-declining species at the HWF Natural Area were long-distance migrants. Chestnut-sided Warbler (*Dendroica pensylvanica*) declined most markedly, followed by Eastern Wood-Pewee (*Contopus virens*), Canada Warbler (*Wilsonia canadensis*), Northern Parula (*Parula americana*), and Wood Thrush (*Hylocichla mustelina*) (Table 1). The top five increasing species were either short-distance migrants or residents and included Brown Creeper (*Certhia americana*), Golden-crowned Kinglet (*Regulus satrapa*), Blue-headed Vireo (*Vireo solitarius*), Hairy Woodpecker, and Yellow-rumped Warbler (*Dendroica coronata*).

TABLE 1. Breeding bird relative abundance, coefficient of variation (CV), and trends in the Huntington Wildlife Forest Natural Area, Newcomb, New York 1954–63 and 1990–2000.

AOU code	Migration status[a]	$\bar{x}$	SD	CV	*P*
YBSA	S	0.46	0.77	158	0.010
HAWO	P	0.43	0.61	131	0.001
EAPE	L	0.93	1.35	106	<0.001
LEFL	L	2.91	1.55	46	<0.001
REVI	L	10.96	2.71	25	0.931
SOVI	S	0.85	1.17	120	<0.001
BLJA	S	0.55	0.94	160	0.003
BCCH	P	0.85	1.29	153	0.690
RBNU	S	0.28	0.69	240	0.102
WBNU	S	0.70	0.89	127	0.326
BRCR	S	0.81	1.12	104	<0.001
WIWR	S	2.75	1.58	56	0.050
GCKI	S	2.91	1.55	27	0.001
SWTH	L	4.45	2.43	54	0.233
WOTH	L	0.81	1.32	137	<0.001
HETH	S	0.75	1.11	149	0.542
NPWA	L	0.18	0.70	382	0.077
CSWA	L	0.40	0.89	187	<0.001
MAWA	L	0.22	0.55	245	0.517
BTBW	L	5.73	2.38	41	0.060
YRWA	S	1.63	1.09	67	0.656
BTGW	L	5.34	1.94	36	0.603
BLWA	L	4.18	2.58	62	0.450
BWWA	L	1.94	0.47	23	0.016
AMRE	L	1.48	1.74	100	<0.001
OVEN	L	7.51	4.10	38	<0.001
CAWA	L	0.45	0.97	194	<0.001
SCTA	L	1.66	1.75	96	<0.001
WTSP	S	0.40	0.72	166	0.001
DEJU	S	1.25	1.37	108	0.072
RBGR	L	0.57	0.84	133	<0.001

[a] L = long-distance migrant, S = short-distance migrant, P = permanent resident.

Comparisons of the HWF Natural Area with Other Data Sets.—Twenty-three of the 31 species (74%) surveyed in both the HWF Natural Area and the BBS had matching regression slope signs (e.g., both trends were increasing or both were decreasing) for the HWF Natural Area and the Adirondack BBS routes, 61% (n = 19) for the Northeastern BBS routes, and 71% (n = 22) for the Eastern BBS routes (Table 2). Fourteen of the 21 species (66%) that occurred both at the HWF Natural Area and Hubbard Brook matched in sign of slope. Surveys at Hubbard Brook and the BBS both began in the 1960s while HWF started in the mid-1950s with a hiatus in counts from 1963 to 1989; not all species surveyed at HWF were surveyed at Hubbard Brook.

TABLE 2. Breeding bird trends in the Huntington Wildlife Forest Natural Area, Newcomb, New York 1954–63 and 1990–2000, and comparison with trends for BBS regions and Hubbard Brook, New Hampshire as reported by Holmes and Sherry (2001).

		HWF Natural Area		BBS Adirondacks			BBS - Region 5 - NE			Hubbard Brook		
AOU code	Migration status[a]	Regression slope	*P*	% change	*P*	Match	% change	*P*	Match	Regression slope	*P*	Match
YBSA	S	−0.028	0.006	2.80	0.060	N	5.60	<0.001	N	−0.028		Y
HAWO	P	0.033	0.006	3.30	0.030	Y	0.80	0.140	Y	−0.014		N
EAPE	L	−0.082	<0.001	−3.70	0.010	Y	−2.30	<0.001	Y			
LEFL	L	−0.015	<0.001	−1.10	0.340	Y	−1.60	<0.001	Y	−0.188	<0.001	Y
REVI	L	0.000	0.981	3.20	0.020	Y	1.40	<0.001	Y	−0.010	<0.05	N
SOVI	S	0.048	<0.001	3.30	<0.001	Y	4.40	<0.001	N	−0.002		N
BLJA	S	−0.011	0.258	0.20	0.860	N	−0.90	<0.001	Y			
BCCH	P	−0.002	0.723	1.80	<0.001	N	1.70	<0.001	N	−0.014		Y
RBNU	S	0.029	0.043	2.00	0.120	Y	2.00	<0.001	Y			
WBNU	S	−0.008	0.281	−0.50	0.820	Y	1.70	<0.001	N	−0.023	<0.05	Y
BRCR	S	0.102	<0.001	0.30	0.890	Y	0.60	0.750	Y	0.013		Y
WIWR	S	0.008	0.058	2.00	0.300	Y	2.70	0.020	Y	−0.012		N
GCKI	S	0.091	0.002	3.00	0.180	Y	4.40	<0.001	Y			
SWTH	L	−0.005	0.138	0.40	0.830	N	0.40	0.710	N	−0.084	<0.001	Y
WOTH	L	−0.066	<0.001	−4.20	<0.001	Y	−2.20	<0.001	Y	−0.118	<0.001	Y
HETH	S	−0.006	0.447	6.10	<0.001	N	3.70	<0.001	N	−0.017		Y
NPWA	L	−0.070	<0.001	2.20	0.450	N	2.50	0.010	N			
CSWA	L	−0.192	<0.001	−2.10	<0.001	Y	−0.70	0.030	Y			
MAWA	L	0.010	0.469	2.10	0.010	Y	3.60	<0.001	Y			
BTBW	L	−0.005	0.066	−1.60	0.090	Y	1.80	0.140	N	0.002		N
YRWA	S	0.033	0.006	2.10	0.010	Y	4.20	<0.001	Y	0.039	<0.01	Y
BTGW	L	−0.001	0.704	0.60	0.520	N	1.10	0.080	N	0.023	<0.001	N
BLWA	L	−0.002	0.387	−0.20	0.850	Y	0.60	0.360	N	−0.056	<0.01	Y
BWWA	L	−0.042	0.016	−1.80	0.080	Y	−1.70	<0.001	Y			
AMRE	L	−0.054	<0.001	−3.20	<0.001	Y	−0.50	0.270	Y	−0.050	<0.001	Y
OVEN	L	−0.021	<0.001	1.10	0.260	N	1.90	<0.001	N	0.013	<0.05	N
CAWA	L	−0.077	<0.001	−5.20	<0.001	Y	−3.20	<0.001	Y			
SCTA	L	−0.023	<0.001	−3.40	<0.001	Y	−0.60	0.010	Y	−0.023	<0.01	Y
WTSP	S	−0.040	0.001	−1.20	0.260	Y	−2.10	<0.001	Y			
DEJU	S	−0.014	0.003	−2.70	0.010	Y	0.00	0.970	N	−0.086	<0.001	Y
RBGR	L	−0.039	<0.001	−3.00	<0.001	Y	−0.40	0.310	Y	−0.052	<0.001	Y

[a] L = long-distance migrant, S = short-distance migrant, P = permanent resident.

DISCUSSION

HWF Natural Area Trends.—A clear pattern of decline among long-distance migrants that breed in the HWF Natural Area emerged when we compared population trends by migration strategy. Only two long-distance migrants, Magnolia Warbler (*Dendroica magnolia*) and Red-eyed Vireo (*Vireo olivaceus*) exhibited non-negative trends. Magnolia Warbler had a positive but non-significant trend while Red-eyed Vireo showed no change. In contrast, the ratio of positive to negative trends among the 14 species of short-distance migrants and permanent residents was approximately 50:50; only three of seven declines were significant, whereas all seven positive trends were significant. These results support those of others that indicate declines in forest birds over the past several decades have involved primarily long-distance migrants (O'Connor 1989, Holmes and Sherry 2001).

HWF Natural Area–Adirondack BBS.—The strength of the association between the two independent surveys, one along road corridors and the other several kilometers from the nearest road, supports the hypotheses that neotropical migrants breeding in the Adirondacks are declining and that those declines have their roots in factors that affect entire regions rather than those factors only affecting individual plots. The pattern of decline for long-distance migrants in the HWF Natural Area is mirrored in the BBS data for the Adirondacks (12 of 15 negative estimates were significant; Table 2). Other studies using BBS trend estimates show that declines in neotropical migrants are profound in the Adirondacks (Partners in Flight 2000). The directions of trends for 13 of the 17 long-distance migrants match when we compare the HWF Natural Area data and BBS data for the Adirondacks. Trends for Swainson's Thrush (*Catharus ustulatus*), Ovenbird (*Seiurus aurocapilla*), Northern Parula, and Black-throated Green Warbler (*Dendroica virens*) do not match, but only two of eight trend estimates for these four species are significant (Ovenbird and Northern Parula, both from the HWF Natural Area).

HWF Natural Area–Northeastern and Eastern BBS.—We found a similar pattern when we compared trends from the HWF Natural Area with regional changes in neotropical migrants, but with proportionally fewer matches (11 of 17 for both Northeastern BBS and Eastern BBS). We expected the HWF Natural Area trends to agree more closely with the Adirondack BBS routes than with those of the larger BBS study regions, which was the case, but the HWF Natural Area trends agreed more closely with those of the Eastern BBS (11 of 14 species) than with the Northeastern BBS (6 of 14). Six of 14 short-distance migrants or permanent residents in the HWF Natural Area matched sign with BBS surveys while trends for 11 of 14 species in the HWF Natural Area matched the Eastern BBS.

HWF Natural Area–Hubbard Brook.—Eleven species of neotropical migrants occurred in both the HWF Natural Area and Hubbard Brook; trends for seven species had matching signs, proportionally fewer matches in sign than with BBS routes. Trends were mismatched for Black-throated Blue Warbler (*Dendroica caerulescens*), Ovenbird, Black-throated Green Warbler, and Red-eyed Vireo. Twelve of the 14 remaining possible trends were significant, and it would appear there is less synchronicity in trends between these two montane, forested sites than between the BBS trends and the HWF Natural Area study site. Holmes and Sherry (2001) demonstrated good correspondence in trends in neotropical migrants on their plot with trends on BBS routes within New Hampshire with nine of 11 species matching in sign.

CONSERVATION IMPLICATIONS

The high correspondence we found in our study between trends from regional BBS routes, and both the HWF Natural Area and Hubbard Brook, indicates that regional rather than local factors may exert the greatest influence on bird populations. Researchers and land managers often conclude that changes in bird populations are driven by local-scale changes in forest age, habitat quality, vegetative composition, dispersion, and location, and these local factors are also responsible for much of the change in regional bird trends. The presence or absence of bird species is in large part based on presence or absence of the core habitat and associated environmental needs for those species. Our research indicates that regional or landscape-scale factors should receive consideration at least equal to that af-

forded local factors when assessing conservation needs for breeding birds, especially long-distance migrants.

The mismatches in sign of trends among the species we investigated could be related to the variability of point counts, differences in detection of bird species, and/or observer bias among sites rather than indicators of a true difference between the bird populations studied. We cannot ascribe the changes in these bird counts to any given factor. Many, mostly unmeasured, potential factors (e.g., changes in foraging substrates, insect outbreaks, increases or decreases in biomass, forest productivity, predator numbers, weather events, changes in vegetative composition and quality) may be driving these changes, and they may be doing so in breeding and wintering areas and/or migration routes.

The data we present from an old growth area distant from roads suggests that BBS surveys may not be as strongly biased by proximity to roads as previously suggested despite potential differences in habitats along roads and those in the HWF Natural Area. The long-term data set on 31 species of birds from the HWF Natural Area allowed for the detection of trends otherwise difficult to identify in bird populations whose sizes typically exhibit high annual variation (Collins 2001).

ACKNOWLEDGMENTS

We thank Deanna K. Dawson, David DeSante, Mercedes Foster, Russell Greenberg, Richard T. Holmes, Annie M. Woods, Benjamin Zuckerberg, and an anonymous reviewer for their helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

American Ornithologists' Union (AOU). 1998. Check-list of North American birds. Seventh Edition. American Ornithologists' Union. Washington, D.C., USA.

Cadman, M. D., H. J. Dewar, and D. A. Welsh. 1998. The Ontario Forest Bird Monitoring Program (1987–1997): goals, methods and species trends observed. Technical Report 325. Canadian Wildlife Service, Ottawa, Ontario, Canada.

Collins, S. L. 2001. Long-term research and the dynamics of bird populations and communities. Auk 118:583–588.

Faaborg, J. 2002. Saving migrant birds: developing strategies for the future. The Corrie Herring Hooks Series. Volume 55. University of Texas Press, Austin, USA.

Faccio, S. D., C. C. Rimmer, and K. P. McFarland. 1998. Results of the Vermont Forest Bird Monitoring Program, 1989–1996. Northeastern Naturalist 5:293–312.

Hagan, J. M., P. S. McKinley, A. L. Meehan, and S. L. Grove. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. Journal of Wildlife Management 61:718–735.

Hedeker, D. and R. D. Gibbons. 1994. A random-effects ordinal regression model for multilevel analysis. Biometrics 50:933–944.

Holmes, R. T. and T. W. Sherry. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. Auk 118:589–609.

Jones, R. H. and D. J. Raynal. 1987. Root sprouting in American beech: production, survival, and the effect of parent tree vigor. Canadian Journal of Forest Research 17:539–544.

Leopold, D. L., C. Reschke, and D. S. Smith. 1988. Old-growth forests of Adirondack Park, New York. Natural Areas Journal 8:166–189.

Link, W. A. and J. R. Sauer. 1998. Estimating population change from count data: application to the North American Breeding Bird Survey. Ecological Applications 8:258–268.

O'Connor, R. J. 1989. Population variation in relation to migrancy status in some North American birds. Pages 64–74 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Editors). Smithsonian Institution Press, Washington D.C., USA.

Partners in Flight. 2000. Partners In Flight Landbird Conservation Plan: Physiographic Area 26: Adirondack Mountains. Draft. American Bird Conservancy, Alexandria, Virginia, USA.

Peterjohn, B. G. 1994. The North American Breeding Bird Survey. Birding 26:386–398.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proceedings of the National Academy of Sciences 86:7658–7662.

Sauer, J. R., J. E. Hines, and J. Fallon. 2001. The North American Breeding Bird Survey, results and analysis 1966–2001. Version 2002.1. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Thompson III, F. R. and M. J. Schwalbach. 1995. Analysis of sample size, counting time, and plot size from an avian point count survey on Hoosier National Forest, Indiana. Pages 45–48 *in* Monitoring bird populations by point counts (C. J. Ralph, J. R. Sauer, and S. Droege, Editors). USDA, Forest Service, General Technical Report PSW-GTR-149. Pacific Southwest Research Station, Albany, California, USA.

Webb, W. L., D. F. Behrend, and B. Saisorn. 1977. Effect of logging on songbird populations in a northern hardwood forest. Wildlife Monographs 55.

The Wilson Journal of Ornithology 120(1):159–166, 2008

TIMING AND LOCATION OF MORTALITY OF FLEDGLING, SUBADULT, AND ADULT CALIFORNIA GULLS

BRUCE H. PUGESEK[1,3] AND KENNETH L. DIEM[2]

ABSTRACT.—We investigated patterns of mortality during post-breeding migrations of California Gulls (*Larus californicus*) nesting near Laramie, Wyoming, USA. We used 151 recoveries and 647 sightings of banded and patagially-marked gulls to compare ratios of mortalities to observations of live birds (1) during four time periods (early and late fall migration, winter, and spring migration), (2) at two locations (Pacific coast and inland), and (3) among three age-classes of gulls (fledglings, 1- and 2-year-olds, and breeding-age adults). Mortality rates were higher in inland areas (35%) than in coastal areas (15%) and were dependent on season within inland areas, but not in coastal areas. Mortality in inland areas during early fall (21%) was comparable with that in coastal areas (13%) but was higher during late fall (68 vs. 13%) and spring migration (46 vs. 17%). Both fledgling (71%) and adult (64%) gulls experienced high mortality rates during late fall migration, possibly because some gulls were too weak to make their way to the Pacific coast and became trapped by poor weather conditions. Adult gulls also experienced high mortality inland during spring migration; few subadults made the costly migration to and from the breeding area. Some adults also skipped breeding and remained in coastal areas during the breeding season. *Received 26 February 2004. Accepted 2 April 2007.*

California Gulls (*Larus californicus*) were first observed and described in California (Baird et al. 1884, Behle 1958). Except for a San Francisco Bay colony, the species breeds inland and spends much of the year away from the Pacific coast. All other breeding colonies are inland and occur from the Salton Sea and Mono Lake, east to the Great Salt Lake, Utah Lake, and Colorado, into the Great Plains of Manitoba and the Dakotas, and north to the Northwest Territories (Cooke 1915, Jehl 1987, Winkler 1996, Molina 2000). The Bamforth Lake, Wyoming population we studied has one of the longer distances to traverse between breeding and wintering areas. This population nests ~130 km east of the continental divide in southeastern Wyoming, more than 1,500 km from the nearest Pacific coastline.

California Gulls at Bamforth Lake follow a triangular migration pattern from breeding areas in Wyoming to wintering areas on the Pacific coast (Pugesek et al. 1999), concentrating between San Francisco and British Columbia. During winter, they move south along the coastline as far as Baja California and return to the Bamforth Lake area to breed, following routes primarily across the southwestern United States.

Previous research on California Gulls nesting at Bamforth Lake demonstrated that survival declines with age (Pugesek and Diem 1990, Pugesek et al. 1995) and is related to increasing reproductive effort with age (Pugesek 1981, 1983, 1987; Pugesek and Diem 1990). We analyzed observation data of banded and wing-marked gulls during migration and wintering periods to further understand costs of migration and its relationship to reproductive effort. We compared ratios of observations of live and dead gulls across seasonal time periods corresponding to post-breeding migration, the wintering period, and spring migration to the breeding colony. We categorized ratios by location of observation (inland and coastal), and among three age-classes of gulls (fledglings, 1- and 2-year-old subadults, and breeding-age adults 3 or more years of age). We hypothesized that: (1) mortality rates in inland areas are higher than in coastal areas, (2) mortality rates in coastal areas are similar among age groups, (3) breeding-age adults experience higher mortality in inland compared with coastal areas during spring and fall migrations, (4) fledglings experience higher mortality in inland compared with coastal areas during their first migration to the coast and do not migrate inland during spring, and (5) subadults remain in coastal areas year-round.

[1] Northern Rocky Mountain Science Center, U.S. Geological Survey-Biological Resources Division, Forest Science Laboratory, 1648 South 7th Street, Bozeman, MT 59717, USA.

[2] Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.

[3] Corresponding author; e-mail: Bruce_Pugesek@usgs.gov

METHODS

Data Collection.—We studied a population of California Gulls banded in Albany County, near Laramie, Wyoming, USA. We banded 9,693 chicks and 1,650 adults between 1958 and 1994 with federal aluminum and monel steel leg bands. We also placed 7.6-cm circular orange patagial markers on 764 chicks and 679 adults from 1966 to 1982. Each marker had a unique symbol and single-digit number painted on both sides. Most gulls were banded and marked at the breeding colony at Bamforth Lake (41° 23′ 39.67″ N, 105° 44′ 13.56″ W). Some (1,203 chicks and 69 adults) were banded at locations within 12 km of this colony. An additional 473 chicks were banded at the Twin Buttes colony (41° 14′ 33.73″ N, 105° 51′ 26.21″ W) on the Laramie plains in 1962 and 1964. The Twin Buttes colony was abandoned in 1964 following 2 years of severe hail storms; the majority of gulls from this colony moved to the Bamforth Lake colony in 1964.

We obtained gull locations from reports sent to us by amateur and professional ornithologists, and from band recovery and return reports from the USGS Bird Banding Laboratory. The information obtained included the patagial marker number and symbol, band number, and the day, month, year, and location of the observation. We converted locations to latitude and longitude coordinates where necessary using NOAA Sectional Aeronautical Charts (1:500,000 for Canada and the United States, and 1:1,000,000 for locations in Mexico). Latitudes and longitudes were entered to the nearest 10 min. Gulls were classified by age by comparing observation dates to our banding records. Henceforth, we use "observation" to refer generically to both reports of live birds and recoveries of bands from dead birds.

Observations were obtained from 1958 to 1994. We removed repeated observations at the same location, 96 observations where age or date of observation was unknown, and observations at the Bamforth Lake colony. We further limited the data set to observations during the migration and winter periods (i.e., Aug through Apr). The final data set consisted of 798 observations of 606 individuals. Full information on age group, season, and location was available for 790 observations. Patagially-marked birds accounted for 630 observations of which 586 were observed alive and 44 were found dead. The remaining 168 observations of banded gulls without wing markers consisted of 61 live birds and 107 found dead.

Data Mapping and Analysis.—We partitioned data into three age groups: fledgling, subadult, and adult. Age was based on the number of years since gulls fledged until the time of the observation. The fledgling age group included all gulls that were <1 year of age. Subadults included all gulls that were >1 but <3 years of age. Adults were ≥ 3 years of age and included all gulls of reproductive age.

We used ARC/INFO software to create location maps (Fig. 1). Observation coordinates of latitude and longitude were rounded to the nearest degree. Polygons were constructed around these 1-degree points and appear rectangular due to the UTM (Universal Transverse Mercator) projection typically used in mapping. Fledglings and subadults were combined into one category, while breeding-age adults (≥ 3 years of age) formed a second category. One observation of a dead fledgling gull in April was not plotted because this individual was observed ~560 km north of Vancouver, British Columbia on the Pacific coast at Greenville Channel (53° 10′ N, 109° 10′ W).

We also partitioned data into four phases of the nonbreeding season: early fall migration (Aug and Sep), late fall migration (Oct through Dec), winter (Jan and Feb), and spring migration (Mar and Apr). We designated locations of observations as being either coastal or inland. The coastal designation refers to lands west of the major mountain chains bounding the Pacific Ocean (Cascades in Oregon and Washington, Sierra Nevada in California, Mohawks in Arizona, and Sierra Madre Occidental in Mexico). Inland locations were east of these mountain ranges.

Given the number of categories, our data were too sparse to apply mark-recapture analysis (Pollock et al. 1990; J. D. Nichols, pers. comm.). Log linear analysis (Jobson 1992) was performed on a matrix of the number of live versus dead bird observations partitioned by age group, season, and location. In log linear analysis, a variety of models composed of main effects and interactions can be tested.

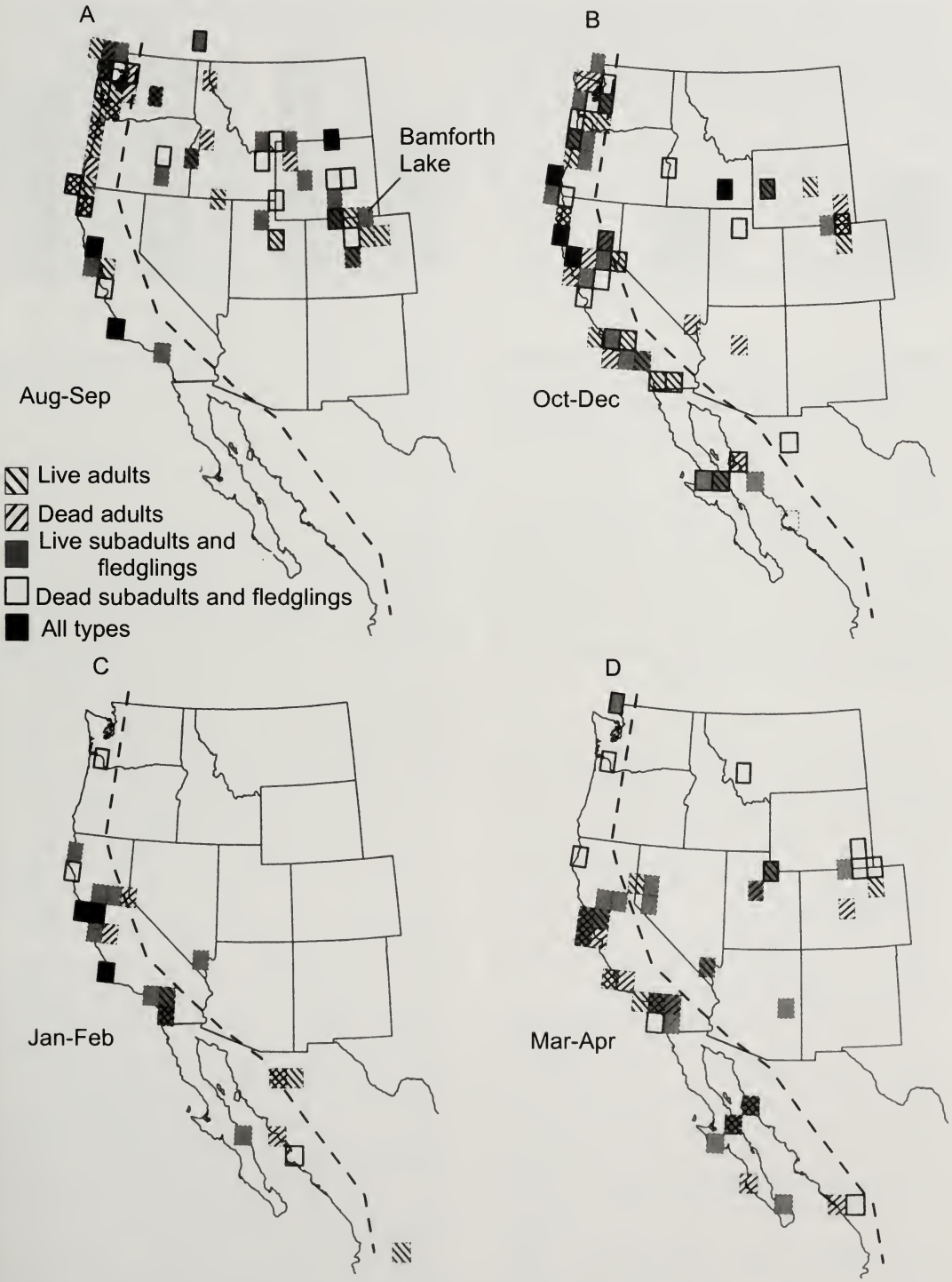


FIG. 1. California Gulls migrate in a triangular pattern with a high proportion of mortalities observed east of the coastal mountain ranges (dashed line) during August through September (A), October through December (B), January through February (C), and March through April (D).

TABLE 1. The only log linear model that fit the California Gull data required a main effect of location, a two-way interaction between age and season, and a three-way interaction between age, season, and location.

Source	df	χ^2	*P*
Location	1	29.98	0.001
Age group × season	6	20.73	0.002
Age group × season × location	6	13.55	0.035
Likelihood ratio	9	14.60	0.100

Model selection was based on an acceptable fit to the data as indicated by a nonsignificant ($P > 0.05$) model likelihood-ratio Chi-square. We began by fitting main effects models and progressed in complexity to models with interactions until a parsimonious model was obtained. Additional Chi-square and Fisher's exact tests were performed on portions of the matrix using, whenever possible, data that were excluded from the log linear analysis because full information was not available for age group, season, or location. Statistical significance was set at $P < 0.05$.

RESULTS

Seasonal Observations.—Observations during early fall (Fig. 1A) included gulls in transit between southeastern Wyoming and the Pacific coast. Large numbers of gulls were already at the coast, including those that did not migrate inland during the breeding season. Most coastal observations were north of San Francisco. Numerous fledglings and adults were also observed in Colorado, south of the breeding island at Bamforth Lake.

Locations of observations shifted during late fall toward greater numbers along the coast south of San Francisco, and there were fewer observations inland (Fig. 1B). Gulls were observed as far south as Baja California, Mexico. Most inland polygons contained observations of dead gulls. During winter, most observations occurred south of San Francisco along the coast (Fig. 1C), and only a few gulls were observed inland, primarily at extreme southerly locations in Nevada and Mexico. One dead adult was found east of the Sierra Nevada Mountains in California. During spring, gulls were observed along migration routes from southerly coastal regions to Bamforth Lake (Fig. 1D). Large numbers of gulls remained along the southern Pacific coast.

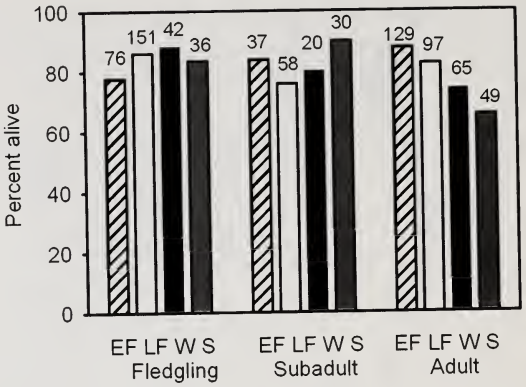


FIG. 2. Fledgling and subadult California Gulls displayed no trend in the percentage of live birds observed through time (EF = early fall, LF = late fall, W = winter, S = spring), but a declining trend was observed among adults. Sample sizes are shown above bars.

Mortality Analysis.—The only log linear model that fit the data included a main effect of location, a two-way interaction between age group and season, and a three-way interaction between age group, season, and location (Table 1). All other combinations of main effects and interactions did not fit the data (maximum likelihood ratio Chi-square, $P < 0.05$). The significant main effect of location resulted from a lower percentage of live birds in inland areas (90 of 139; 65%) compared with coastal areas (557 of 659; 85%); data pooled across time period and age groups ($\chi^2 = 29.26$, df = 1, $P < 0.001$).

The significant age group × season interaction was largely a consequence of seasonal variation observed among adults. The percentage of live observations did not differ across time periods among fledglings ($\chi^2 = 3.31$, df = 3, $P = 0.35$), or subadults ($\chi^2 = 2.80$, df = 3, $P = 0.42$) but declined among adult gulls with each time period ($\chi^2 = 13.30$, df = 3, $P = 0.004$; Fig. 2). The lowest percentage of observations of live adult gulls occurred during spring migration.

The significant three-way interaction among season, age group, and location (Table 1) resulted from (1) a consistently high percentage of live birds in coastal areas across all seasons and age groups, and (2) a lower percentage of live birds in inland areas compared

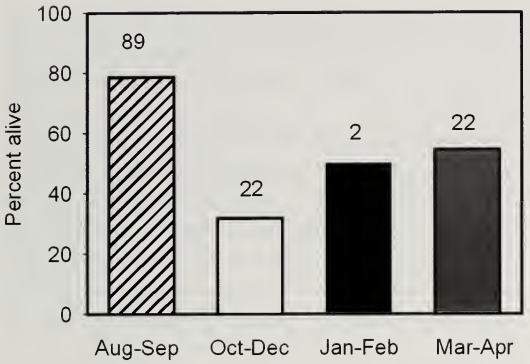


FIG. 3. Mortality among California Gulls in inland areas is high during migrations. Sample sizes are shown above bar.

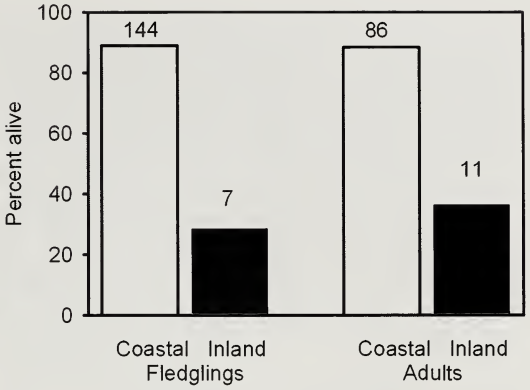


FIG. 4. Mortality among fledgling and adult California Gulls during late fall is higher in inland areas (solid bars) compared with coastal areas (open bars). Sample sizes are shown above bar.

with coastal areas, primarily in late fall and spring due to a low percentage of live fledglings during fall migration, and a low percentage of live adults observed during spring and fall migrations.

Analysis of the coastal location with all age groups pooled indicated high percentages of live birds in all seasons ($\chi^2 = 4.13$, df = 3, $P = 0.25$; early fall: 87%, $n = 153$; late fall: 87%, $n = 284$; winter 80%, $n = 125$; spring: 83%, $n = 93$). There were no differences across seasons in percent live birds in the coastal area for fledglings ($\chi^2 = 2.07$, df = 3, $P = 0.56$), subadults ($\chi^2 = 2.48$, df = 3, $P = 0.48$), or adults ($\chi^2 = 6.66$, df = 3, $P = 0.084$). The lowest percentage of live adults (75%) occurred in winter.

The percentage of live birds observed in inland areas was lower compared with coastal areas in late fall ($\chi^2 = 44.03$, df = 1, $P < 0.001$) and spring ($\chi^2 = 8.11$, df = 1, $P = 0.004$). There were 247 live and 37 dead observations (87%) in coastal areas, and 7 live and 15 dead observations (32%) during late fall. During spring, there were 77 live and 16 dead observations (83%) in coastal areas, and 12 live and 10 dead observations (54%) at inland areas. During early fall, there was a slightly higher percentage of gulls alive in coastal areas (87%, $n = 153$) compared with inland areas (79%, $n = 89$), but the difference was not significant ($\chi^2 = 2.85$, df = 1, $P = 0.091$). During winter, too few birds were observed inland for statistical analysis. There were 100 live and 25 dead bird observations in coastal areas (80%), and 1 live and 1 dead bird observations (50%) at inland areas.

Percentages of gulls observed alive at inland locations differed with season ($\chi^2 = 19.48$, df = 3, $P < 0.001$) (Fig. 3). The highest percentage alive occurred during early fall and the lowest percentage occurred during late fall.

Too few subadults were observed inland in all time periods to analyze statistically. The only times sufficient fledglings were present inland was during early and late fall. In both early and late fall, the percentage of live fledglings was lower inland (63%, $n = 19$) than on the coast (83%, $n = 57$), but the difference was only significant in late fall (early fall: $\chi^2 = 3.06$, df = 1, $P = 0.093$; late fall: Fisher's exact test, two-tailed probability, $P < 0.001$; Fig. 4). A similar pattern was observed among adult gulls (early fall: coastal: 89%, $n = 63$; inland: 86%, $n = 63$; $\chi^2 = 0.19$, df = 1, $P = 0.66$) (late fall: $\chi^2 = 18.25$, df = 1, $P < 0.001$; Fig. 4). Too few adults were observed inland in winter for statistical analysis. In spring, the percentage of live adults inland, 5 of 15 (33%), was significantly lower ($\chi^2 = 9.75$, df = 1, $P = 0.002$) than in coastal areas, 27 of 34 (79%).

We combined data for early and late fall, and found that a significantly lower ($\chi^2 = 5.14$, df = 1, $P = 0.023$) percentage of fledglings (56%; $n = 27$) was observed alive than adults (78%; $n = 78$) (fledglings: 15 of 27; adults 61 of 78).

DISCUSSION

Comparing percentages of observations of live and dead birds is not equivalent to mark-recapture and other survival estimation methods (Pollock et al. 1990). These comparisons do not provide precise survival estimates, but can be used to compare categories to illustrate when and where gulls experience greater or lesser amounts of mortality. Mark-recapture estimates of survival of breeding-age adult California Gulls in the Bamforth Lake population ranged from 88% among 3-year-old gulls to 76% among the oldest gulls (≥20 years of age; Pugesek et al. 1995). The bulk of our population was <12 years of age (BHP, pers. obs.) and the overall survival rate of breeding-age adults is likely in the range of 82–87%. This survival rate is similar to our percent alive values for adult gulls, but we have no theoretical basis for claiming equivalency between survival rate estimates and our percent alive estimates.

Data on the location of both live and dead gulls, and dates of observation of live gulls are precise because they are based on direct observations by qualified observers. Data on time of observation of dead gulls are less accurate because we have no way of knowing how long the gull had been dead before it was located. Thus, tabulations of seasonal categories are biased toward shifting the time of death into a later time category. This inherent bias is probably unimportant because gulls are absent from areas critical for analysis during most periods other than the time to which they were assigned. For example, gulls found dead inland in spring likely died then because they are largely absent from the area in all other time periods. The same is true for gulls observed inland during the post-breeding fall migration to the Pacific coast. Some bias may occur, however, as a result of incorrectly assigning observations to late fall when death occurred in the early fall.

The sample revealed no differences in the percentage of live gulls observed across age groups. When the sample was additionally categorized by season, we found that adults incurred relatively high mortality during spring migration.

The percentage of live gulls observed in coastal areas remained high during all seasons, 80–87% among all age groups combined. No significant variation within age groups was detected in percent live gulls in coastal areas.

Fledglings of other gull species experience high mortality and subadult mortality is greater than adult mortality but is more similar to adult than fledgling mortality (Coulson and Wooller 1976, Bradley et al. 1989). Our results of high fledgling mortality are congruent with these findings. Fledgling mortality occurs during their first migration, exceeding that of adult gulls; thereafter, in coastal areas, fledgling mortality is similar to that of older gulls. The offspring of older parents grow more rapidly and over a longer duration of parental care compared with offspring of younger parents (Pugesek 1995). This may translate into a lower mortality rate during fall migration and an overall higher fledgling survival rate among the offspring of older parents.

Patterns of observations in inland areas indicated that migrations through these areas resulted in high mortality during spring and fall. The majority of juveniles left the Bamforth Lake area after fledging and remained in coastal areas until they were of breeding age. Subadults also remained in coastal areas year-round. One-year-old gulls are rarely observed and 2-year-olds are infrequently observed in the Bamforth Lake and surrounding area during summer months (BHP, pers. obs.).

Our results are consistent with earlier findings of cost of reproduction for California Gulls at Bamforth Lake measured in terms of reduced survival (Pugesek 1987, Pugesek and Diem 1990). As gulls age, they (1) skip breeding less frequently (Pugesek and Wood 1992), (2) exert higher levels of reproductive effort when breeding (Pugesek 1981, 1983), and (3) produce more offspring (Pugesek and Diem 1983). Those gulls that skip breeding increase their prospects for survival by remaining in coastal areas, thereby avoiding inland migrations to and from the breeding colony. Our observations of mortality among adults during the breeding season are insufficient to explain the declines in survival rate associated with high numbers of offspring fledged (Pugesek and Diem 1990, Pugesek et al. 1995) and longer durations of parental care (Pugesek 1987). Few adult deaths were observed during the breeding season (Pugesek 1983). We suggest

the reduced survival rates among gulls that fledged greater numbers of offspring over longer durations of parental care were due to higher mortality during the fall migration. This is true for older gulls, in particular, those that lose greater amounts of body mass during the breeding season compared with younger gulls (Pugesek and Diem 1990). We hypothesize that gulls that lose high amounts of body mass during the breeding season may be required to remain in inland areas longer after the breeding season to regain their physical condition but may be trapped in late fall before they can return to the Pacific coast. There is potential bias in categorizing time of death, but we note that large numbers of gulls remained in southeastern Wyoming and in Colorado, while other gulls were on migration routes to the Pacific coast.

If physical exhaustion prior to migration is a key source of reproductively-induced mortality, California Gulls at Bamforth Lake are probably on the extreme end of a severity scale for this phenomenon. Gulls typically arrived in the Bamforth Lake area for the breeding season before snow cover dissipated and lakes thawed. The Bamforth Lake area also provided severe thermal stress. During the territorial and egg-laying phases of reproduction, gulls were frequently exposed to average daily wind chills in excess of −20° C (BHP, unpubl. data) and June snowstorms were a common event. By late summer, gulls captured using cannon nets were frequently in poor physical shape as evidenced by sunken, boney keels and low body mass (Pugesek and Diem 1990). Finally, the post-breeding migration to the Pacific coast is longer for gulls east of the Continental Divide. Populations with a less stressful nesting habitat and a shorter migration may experience lower reproductively-induced mortality compared with the Bamforth Lake population.

Under the circumstance of high reproductively-induced mortality, we expect that selection pressures for increasing reproductive effort with age are stronger in the Bamforth Lake population compared with populations nesting near the Pacific coast or in less stressful habitats. It would be of interest to compare life history characteristics among populations of California Gulls, for example, those nesting west of the Continental Divide with those nesting east of the divide where migrations are longer and environmental stress is likely harsher. Those nesting east of the Continental Divide may exhibit greater age-specific variation in egg mass, clutch size, fledging success, age at first breeding, frequency of skipped breeding attempts, and age-specific variation in survival rates. Also, behavioral measures which are indicative of reproductive effort such as nest defense rates (Pugesek 1983) can be easily duplicated and compared among populations.

ACKNOWLEDGMENTS

Our research was supported by grants from NSF (DEB 791997), Sigma Xi, Wilson Ornithological Society, Chapman Foundation, and NIA (T32-AG00110-03). We thank the U.S. Fish and Wildlife Service, Arapaho National Wildlife Refuge, and Wyoming Game and Fish Department for cooperation. We especially thank C. R. Corne for developing and testing the data base for the analysis. J. R. Jehl Jr., R. M. Erwin, and one anonymous reviewer provided helpful comments.

LITERATURE CITED

Baird, S. F., T. M. Brewer, and R. Ridgway. 1884. The waterbirds of North America. Volume 2. Memoirs of the Museum of Comparative Zoology at Harvard College 13:1–549.

Behle, W. H. 1958. The bird life of the Great Salt Lake. University of Utah Press, Salt Lake City, USA.

Bradley, J. S., R. D. Wooller, I. J. Skira, and D. L. Serventy. 1989. Age-dependent survival of breeding Short-tailed Shearwaters *Puffinus tenuirostris*. Journal of Animal Ecology 58:175–188.

Cooke, W. W. 1915. Distribution and migration of North American gulls and their allies. U.S. Department of Agriculture Bulletin 292.

Coulson, J. C. and R. D. Wooller. 1976. Differential survival rates among breeding Kittiwake Gulls *Rissa tridactyla* (L.). Journal of Animal Ecology 45:205–214.

Jehl Jr., J. R. 1987. Geographic variation and evolution in the California Gull (*Larus californicus*). Auk 104:421–428.

Jobson, J. D. 1992. Applied multivariate data analysis. Volume II. Categorical and multivariate methods. Springer-Verlag, New York, USA.

Molina, K. C. 2000. The recent nesting of California and Laughing gulls at the Salton Sea, California. Western Birds 31:106–111.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107.

Pugesek, B. H. 1981. Increased reproductive effort

with age in the California Gull (*Larus californicus*). Science 212:822–823.

PUGESEK, B. H. 1983. The relationship between parental age and reproductive effort in the California Gull (*Larus californicus*). Behavioral Ecology and Sociobiology 13:161–171.

PUGESEK, B. H. 1987. Age-specific survivorship in relation to clutch size and fledgling success in California Gulls. Behavioral Ecology and Sociobiology 21:217–221.

PUGESEK, B. H. 1995. Chick growth in the California Gull: reproductive effort versus foraging efficiency hypotheses. Animal Behaviour 49:641–647.

PUGESEK, B. H. AND K. L. DIEM. 1983. A multivariate study of the relationship of parental age to reproductive success in California Gulls. Ecology 64: 829–839.

PUGESEK, B. H. AND K. L. DIEM. 1990. The relationship between reproduction and survival in known-aged California Gulls. Ecology 71:811–817.

PUGESEK, B. H. AND P. K. WOOD. 1992. Alternate reproductive strategies in the California Gull. Evolutionary Ecology 6:279–295.

PUGESEK, B. H., K. L. DIEM, AND C. L. CORDES. 1999. Seasonal movement, migration, and home ranges of immature and adult California Gulls nesting at Bamforth Lake, Wyoming. Colonial Waterbirds 22:29–36.

PUGESEK, B. H., C. NATIONS, K. L. DIEM, AND R. PRADEL. 1995. Mark-resighting analysis of a California gull population. Journal of Applied Statistics 22:625–639.

WINKLER, D. W. 1996. California Gull (*Larus californicus*). The birds of North America. Number 259.

The Wilson Journal of Ornithology 120(1):167–175, 2008

EFFECTS OF PREDATION AND FOOD PROVISIONING ON BLACK TERN CHICK SURVIVAL

SHANE R. HEATH[1,2,3] AND FREDERICK A. SERVELLO[1]

ABSTRACT.—We placed predator exclosures around 31 Black Tern (*Chlidonias niger*) nests in Maine in 2001–2002 to measure growth and survival of chicks. Fifty-four percent of exclosed nests that hatched young were depredated in 2001 and four exclosed nests were abandoned prior to hatch. We modified our exclosure design in 2002 and only one nest (7%) was depredated and no nests were abandoned prior to hatch. Kaplan-Meier estimates of chick survival in the absence of predation were 0.87 to 18 days in 2001 and 0.90 to 15 days in 2002. Mass ratios among first, second, and third-hatched chicks indicated that size hierarchies were present in broods near time of brood completion, but linear growth rates and asymptotic mass were not affected by hatch order in 2- or 3-chick broods. Predation was the primary determinant of chick survival in Black Tern colonies studied and food availability was not limiting chick growth. Predator exclosures did not prevent all depredation, but our exclosure design was effective at protecting and retaining chicks until fledgling age at 70% of nests; the majority of adults readily accepted predator exclosures. *Received 23 December 2006. Accepted 19 April 2007.*

Black Terns (*Chlidonias niger*) are listed as endangered, threatened, or a species of concern in multiple states (USA) and Canadian provinces (Shuford 1999), and populations declined 3.1% annually during 1966–1996 in North America (Peterjohn and Sauer 1997). Low breeding productivity may be a key factor limiting population growth (Servello 2000), especially among small, isolated populations along the southern portion of this species' range. Nest success in this species is well studied (reviewed in Servello 2000), but chick survival estimates are lacking. Monitoring chick survival for wetland-nesting terns is problematic because chicks use dense vegetation for cover and leave nests soon after hatching (Hall 1988, Cuthbert and Louis 1993). Thus, few studies have reported chick survival rates or investigated factors contributing to chick mortality (Servello 2000). Fewer than 100 pairs of Black Terns nest annually in Maine and chick survival appears to be the primary cause of low breeding success (F. A. Servello, unpubl. data). Identifying factors contributing to chick mortality is critical for understanding Black Tern ecology and developing management strategies for increasing recruitment.

Black Terns nest in wetlands where a wide variety of predators commonly occur. Reports of predation on Black Tern chicks have been limited to chicks held in small enclosures (Dunn 1979, Chapman and Forbes 1984) or anecdotal observations (Shealer and Haverland 2000). Low food availability or inadequate provisioning by adults may be a common cause of chick mortality in Black Terns (Mosher 1986, Beintema 1997) as in other tern species (Safina et al. 1988, Monaghan et al. 1989, Nisbet et al. 1998, Eyler et al. 1999). However, food limitation in Maine colonies has not previously been observed (Gilbert and Servello 2005). Black Terns exhibit laying and hatching asynchrony (Dunn and Agro 1995), which produces a size hierarchy among siblings and can result in lower growth and survival rates for the youngest chicks in broods when food resources are scarce (Langham 1972, Skagen 1988, Bollinger et al. 1990, Brown and Morris 1996). We hypothesize that predation is the primary factor contributing to chick mortality of Black Terns in Maine, but annual or local variation in food availability may also have a contributing role.

Predator exclosures have been successfully used with shorebirds to prevent egg depredation (Rimmer and Deblinger 1990, Estelle et al. 1996, Mabee and Estelle 2000, Larson et al. 2002), but have not been designed to protect chicks. With terns, smaller retention fenc-

[1] Department of Wildlife Ecology, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA.

[2] Current address: Institute for Wildlife Studies, 2515 Camino del Rio S, Suite 334, San Diego, CA, 92108, USA.

[3] Corresponding author; e-mail: shaneheath1@gmail.com

es have frequently been used to confine chicks, including those of Black Terns, for research purposes (e.g., monitoring growth, survival, feeding behavior) but not for predator deterrence (Morris et al. 1976, Burger et al. 1996, Robinson and Hamer 2000, Shealer and Haverland 2000, Gilbert and Servello 2005). We sought to develop a predator exclosure that would hold chicks until fledging, deter mammalian and avian predators, and be suitable for wetland substrates while simultaneously allowing unimpeded feeding and brooding by adults. A useful exclosure would also provide opportunities for research on chick predation and growth. We report on the efficacy of our predator exclosures and test two hypotheses: (1) predator exclusion would result in chick survival near 100% if predation was the principal mortality factor and (2) growth rates of Black Tern chicks would decrease with hatch order and increasing brood size if food provisioning was inadequate.

METHODS

Study Area.—This study was conducted at three Black Tern breeding colonies (Carlton Pond, Douglas Pond, and Messalonskee Lake) in Maine, USA, in May–July 2001–2002. Carlton Pond (44° 40′ N, 69° 15′ W) had a total area of 431 ha and included 75 ha of semi-permanent emergent wetland bordering 113 ha of open water with dense mats of floating-leaf vegetation. Nesting areas were dominated by sedges (*Carex* spp.), *Sphagnum* spp., and pickerelweed (*Pantedaria cordata*). Douglas Pond (44° 50′ N, 69° 21′ W) was an impounded wetland on the Sebasticook River and had a total area of 227 ha, which included 44 ha of semi-permanent emergent vegetation bordering 85 ha of open water. Nesting areas at Douglas Pond were dominated by river bulrush (*Scirpus* spp.) or sedges. Messalonskee Lake (44° 26′ N, 69° 49′ W) was a large lake (1,786 ha) with 55 ha of semi-permanent emergent wetland at one end; nesting areas were dominated by sedges and *Sphagnum* spp.

Field Procedures.—We constructed 17 predator exclosures around individual nests in 2001 and 14 exclosures around nests in 2002. Black Terns differ from other species for which nest exclosures have been constructed in that adults fly rather than walk into exclosures, and our design had to accommodate this behavioral difference. Predator exclosures consisted of two primary parts: (1) a circular fence 1 m in diameter and 0.3 m in height placed around the nest (chick retention fence), and (2) a circular fence 4.6 m in diameter and 1.4 m in height, placed concentrically around the retention fence (predator exclusion fence; Fig. 1). Landscaping cloth was attached to the inside of the chick retention fences to a height of 0.15 m and to the outside of the predator exclusion fences to a height of 0.9 m prior to deployment (Fig. 1). In addition, the retention fences had a 10–15 cm wide flap of chicken wire wrapped with landscaping cloth ("concealment flap") attached inside the retention fence at a height of 0.15 m to provide overhead concealment. The purposes of the retention fence were to reduce predation risk by limiting movements of chicks, keeping chicks from exclosure fences, and providing a location for horizontal and overhead concealment of chicks. The landscaping cloth in retention fences also prevented chicks from climbing out of the enclosure. The purposes of the exclusion fence were to reduce predator access and reduce visibility of chicks to ground predators. We deployed retention fences around nests during the second half of incubation, and installation took less than 3 min. Retention fences were held tightly to the substrate with three wooden stakes. The "concealment flaps" were initially pressed flat against the retention fence until clutches hatched.

We avoided hot sunny days when deploying exclosures to avoid egg heating while adults were acclimating to the structure. We removed eggs and placed them in an insulated container during erection of the exclusion fence. Exclusion fencing was typically deployed 3–4 days after the retention fencing, but before eggs hatched to allow terns to acclimate to these structures. However, retention and exclosure fences in 2001 were installed simultaneously at four nests and exclusion fencing was installed after hatch at two nests in 2002. Two to four people were required to erect predator exclusion fencing and construction time was typically 15–25 min depending on water depth. Water depths were typically 0.2 to 1.0 m. Eight to 10 wooden stakes (2 m in length) were used to support exclusion fences and hold them flush to the substrate, and four rope guidelines attached to smaller stakes were

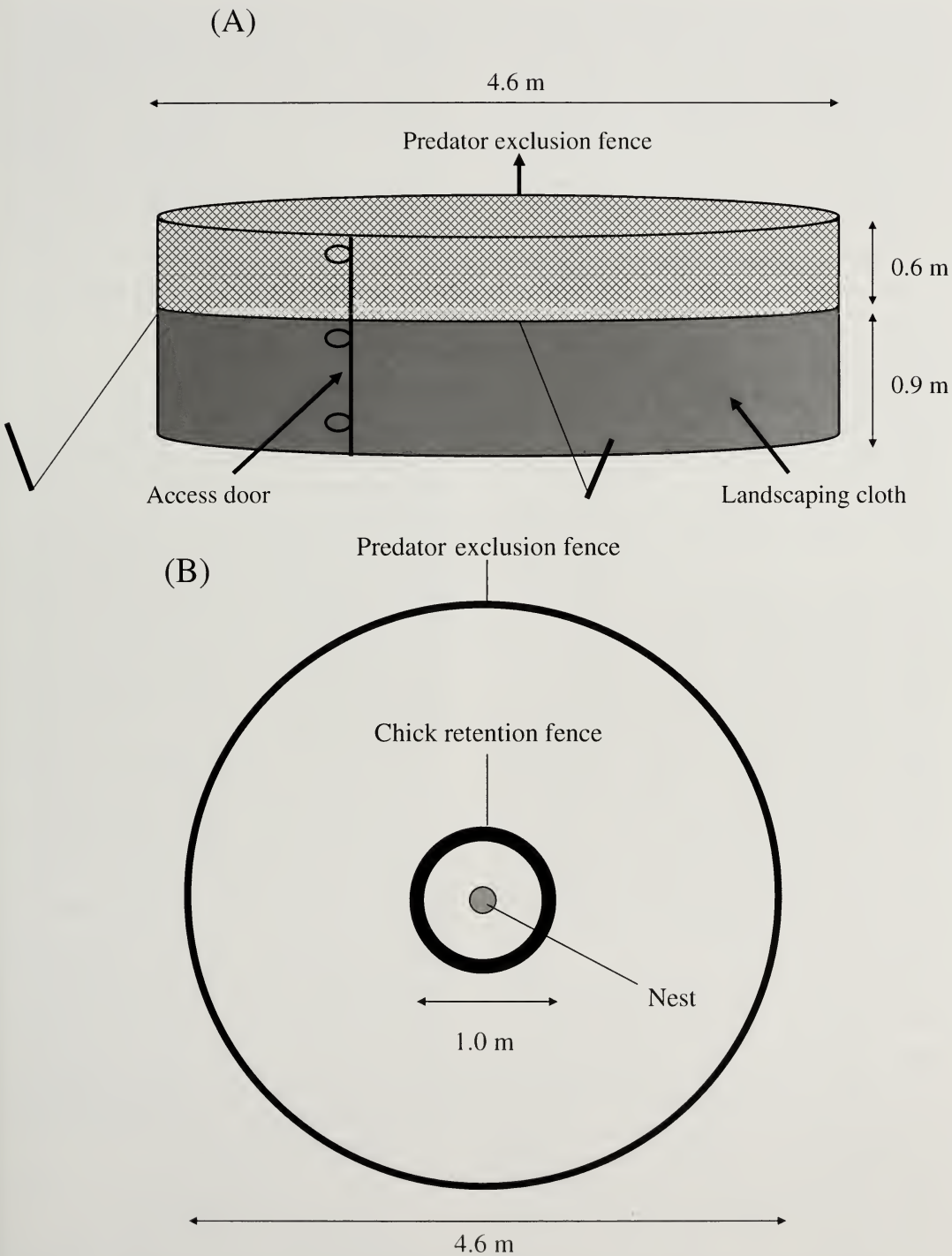


FIG. 1. (A) Predator exclusion fence including landscaping cloth, rope and stakes, and researcher access door, and (B) diagram showing predator exclosure around Black Tern nest, including predator exclusion and chick retention fences.

used to add tension and reduce movement by strong winds (Fig. 1). The skirt of landscaping cloth was partially submerged under the extant water along with the lower portion of the fence to serve as an additional ground-level barrier. The two ends of the exclusion fencing, overlapped and fastened together with removable wires, served as the entrance for researchers.

We selected entire clusters of nests or individual nests on colony edges for predator exclosures to allow repetitive access to nests without major disturbance to colonies. We visited exclosures approximately every 1–2 days to document hatching and to inspect exclosures. Chicks at each nest were assigned an alpha code based on hatch order: A-chick = first hatched, B-chick = second hatched, C-chick = third hatched. We visited exclosures to weigh chicks every 2 days following hatch, on average. Chicks missing from exclosures prior to the anticipated fledge dates were considered depredated if no means of escape were evident. Dead chicks were removed from the exclosures to avoid attracting predators. We retained broods in 2001 until A-chicks reached an approximate fledging age of 18 days (Dunn and Agro 1995) except when they flew from exclosures. We released broods in 2002 when A-chicks reached 15 days of age to reduce potential losses of older chicks to predators. Chicks became more active (increased wing flapping, vocalizations) at this age (Dunn 1979) and appeared to be more vulnerable to predators at older ages in exclosures during 2001.

Statistical Analyses.—We calculated Kaplan-Meier survival estimates for non-depredated chicks by censoring depredated, escaped, or released chicks in analyses (Pollock et al. 1989). We compared survival rates between years using log-rank tests (Pollock et al. 1989). We calculated mass ratios of chicks for each nest with a predator exclosure to examine if size hierarchies were established by hatch order. Mass ratio is an index of the competitive ability of the latter-hatched chicks relative to the A-chick during the early post-hatch period (Bollinger 1994). We defined mass ratio as a chick's mass divided by the mass of the A-chick following brood completion (modified from Bollinger 1994). Brood completion occurred when the final chick of each brood hatched. Mass ratios of B- and C-chicks were compared using ANOVA. B- or C-chicks were assumed to differ from A-chicks if 95% CIs for their mass ratios did not include 1.0. We used linear regression analysis to calculate linear growth rate (LGR; Emms and Verbeek 1991) for each chick for the age period 2–11 days when Black Tern chick growth is approximately linear (Beintema 1997). Only chicks with a minimum of three mass measurements during this interval were included. We iteratively fit the logistic equation,

$$\text{Chick mass} = \text{AM}/\{1 + \exp[-K\cdot(\text{age} - t_0)]\},$$

to growth curves of individual chicks to estimate asymptotic mass (AM), where K is a growth coefficient and t_0 is time of inflection (Starck and Ricklefs 1998). We only calculated AM for chicks that reached 13 days of age because weight measurements approaching the asymptote are required (Ricklefs 1967). Chick weights from broods that were eventually depredated were included if meeting the above criteria for all growth analyses (mass ratio, LGR, AM).

We analyzed data for 2- and 3-chick broods separately. We only included 2-chick broods if they resulted from a 2-egg clutch or the failure of the third egg to hatch; broods that lost a chick from a 3-chick brood were excluded. We used linear regression to examine relationships of LGR and AM with hatch date. We first examined effects of colony and year on LGR using ANOVA, and then pooled data across colonies and years to separately examine the dependence of LGR and AM on hatch order and brood size using nested ANOVA (with brood as the nested term). Year and colony effects were analyzed separately because small sample sizes precluded tests of year by colony interactions.

RESULTS

Predator Exclosures.—Four nests did not hatch in 2001 and were abandoned (Table 1). Three of these nests were abandoned immediately after exclusion fencing was erected, while the fourth nest was incubated past the expected hatch date and eventually abandoned. Hatching success of nests incubated to

TABLE 1. Success of Black Tern nests with predator exclosures in Maine wetlands, 2001–2002. Hatching success is defined as the proportion of eggs hatched.

Year	Colony	Nests exclosed	Nests hatched (eggs)	Eggs hatched	Hatching success (%)
2001	Carlton	6	5 (15)	15	100
	Douglas	6	4 (12)	11	92
	Messalonskee	5	4 (10)	10	100
	Totals	17	13 (37)	36	97
2002	Carlton	9	9 (26)	18	69
	Douglas	5	5 (15)	15	100
	Totals	14	14 (41)	33	81

term was 97% in 2001 and 36 eggs hatched (Table 1). Seven (54%) of 13 nests with young were depredated with 17 chicks lost (Table 2). The two depredated exclosures at Carlton contained three 16-day-old chicks and one 14-day-old chick, respectively, while the depredated exclosure at Douglas contained three chicks less than a week old. All four nests that hatched at Messalonskee were depredated within a 3-day period. These four depredated exclosures contained three 15-day-old chicks, three 16-day-old chicks, two 10-day-old chicks, and two 6-day-old chicks, respectively. Overall, three chicks from three different broods died of causes unrelated to predation (Table 2). Sixteen chicks were released from exclosures in 2001 (Table 2).

No nests were abandoned prior to hatch in 2002. Hatching success of nests incubated to term was 81% in 2002 and 33 eggs hatched (Table 1). Hatching success of exclosed nests at Carlton was 69%, but 100% at Douglas (Table 1). At Carlton, the third egg of a 3-egg clutch failed to hatch at three nests, and another nest containing one chick and two intact eggs was abandoned. One nest (7%) was depredated at Carlton in 2002 resulting in loss of three chicks <1 week of age. Three chicks from three different broods died of causes unrelated to predation, while one brood of three chicks escaped their exclosure prior to fledging age (Table 2). Twenty-four chicks were released from exclosures in 2002 (Table 2). Predators entering exclosures were not identified in either year.

Survival of Non-depredated Chicks.—Six chicks from six different broods died within exclosures in a manner unrelated to predation. Two of these chicks were <5 days of age and were found dead outside of the retention fencing. These chicks may have escaped from the retention fence and perished after becoming separated from their respective broods, or may have died and been removed from the nest by the adults. Two other chicks died after apparent abandonment by adults, most likely as a result of investigator disturbance associated with predator exclosures. The remaining two chicks, a 16-day-old B-chick and an 8-day-old C-chick, were both in 3-chick broods and exhibited normal growth for 12 and 6 days, respectively, before declining in mass prior to

TABLE 2. Fate of Black Tern chicks in predator exclosures, including cause of loss, 2001–2002.

Year	Colony	Chicks depredated (nests)	Chicks died of other causes (nests)	Chicks escaped from exclosure (nests)	Chicks released from exclosures (nests)
2001	Carlton	4 (2)	2[a] (2)	0	9 (3)
	Douglas	3 (1)	1[b] (1)	0	7 (3)
	Messalonskee	10 (4)	0	0	0
	Totals	17 (7)	3 (3)	0	16 (6)
2002	Carlton	0	3[c] (3)	0	15 (8)
	Douglas	3 (1)	0	3 (1)	9 (3)
	Totals	3 (1)	3 (3)	3 (1)	24 (11)

[a] One chick was found dead outside of retention fencing and one chick died of apparent starvation.
[b] Chick found dead outside of retention fencing.
[c] Two chicks from two separate broods died after apparent abandonment by adults, while the third chick died of apparent starvation.

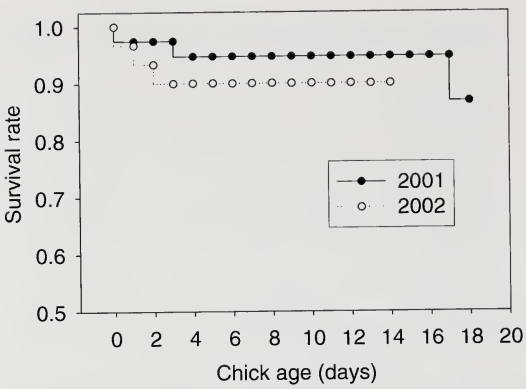


FIG. 2. Kaplan-Meier survival rates for Black Tern chicks not depredated in predator exclosures in 2001–2002 at Douglas Pond and Carlton Pond, Maine. Estimates were based on 17 chicks from six broods in 2001 and 27 chicks from 13 broods in 2002.

death. Including the above instances of mortality, chick survival (±SE) to 18 days in 2001 in the absence of predation was 0.87 ± 0.08 (95% CI: 0.71–1.03) and 0.90 ± 0.05 (95% CI: 0.80–1.00) to 15 days in 2002 (Fig. 2) and did not differ among years ($P = 0.46$).

Growth Analyses.—Nineteen broods (3-chick broods, $n = 13$; 2-chick broods, $n = 6$) were used in growth analyses. Mass ratios differed ($F_{1,24} = 11.38$, $P = 0.003$) between B- and C-chicks in 3-chick broods. B-chicks were on average 91% of the mass of A-chicks ($n = 13$, 95% CI = 0.83–0.98) near time of brood completion and C-chicks were 73% of the mass of A-chicks ($n = 13$, 95% CI = 0.65–0.82). In 2-chick broods, B-chicks were on average 72% of the mass of A-chicks ($n = 6$, 95% CI = 0.59–0.86) near brood completion.

Neither LGR ($P = 0.10$, $n = 51$, $r^2 = 0.034$) nor AM ($P = 0.48$, $n = 43$, $r^2 = 0.001$) were affected by hatch date. Estimates of LGR for individual chicks ranged from 3.22 to 5.87 g/day, with a mean of 4.47 g/day. Colony ($F_{2,10} = 0.24$, $P = 0.79$) and year ($F_{1,11} = 1.31$, $P = 0.28$) did not affect LGR; therefore, data were pooled across years and colonies to test hatch order effects. Linear growth rates were not affected by hatch order for either 3-chick broods ($F_{2,24} = 2.13$, $P = 0.14$) or 2-chick broods ($F_{1,5} = 1.06$, $P = 0.35$). Growth rates did not differ ($F_{1,32} = 1.33$, $P = 0.26$) with brood size. Estimates of AM for individual chicks ranged from 39.0 to 73.5 g, with a mean of 61.6 g. Asymptotic mass did not differ among colonies ($F_{2,8} = 1.21$, $P = 0.35$) or years ($F_{1,9} = 1.00$, $P = 0.34$) and data were pooled across years and colonies to test for hatch order effects. Asymptotic mass did not differ by hatch order for 3-chick broods ($F_{2,20} = 0.71$, $P = 0.50$). We did not test effects of hatch order on AM for 2-chick broods because of small sample sizes.

DISCUSSION

Predator Exclosures.—Our predator exclosure design was not effective in excluding predators in 2001, but after our modifications we observed lower predation in 2002. However, it is unknown if this lower predation (7%) resulted from our modifications or from changes in predator abundance between years. Adult terns generally accepted the small retention fences relatively quickly (3–15 min), but were more hesitant to initially enter the larger exclosures. Adults frequently circled the structure for >20 min. Once acclimated, adults appeared to travel normally to and from the nest during incubation and chick feeding. Four nests in 2001 were abandoned prior to hatch following deployment of predator exclusion fencing. Retention and exclusion fencing were erected simultaneously at two of these nests, resulting in immediate abandonment. The predator exclusion fences at all four abandoned nests were erected ≥6 days prior to hatch, which may have been too early. The willingness of adult Black Terns to leave their nests for extended periods decreases as the incubation period lengthens (Cuthbert 1954) suggesting that adult acceptance of exclosures may increase closer to hatching. Nests where exclusion fences were constructed just before or immediately following hatch were not abandoned and we conclude this is the optimal time for deployment. We do not recommend deploying retention fencing and predator exclusion fencing on the same day.

Predators successfully entered more than half of all exclosures where eggs hatched in 2001. A high proportion of depredated chicks were relatively old (58% at 14–17 days of age) suggesting that older chicks in exclosures may be susceptible to loss as they approach fledging. Chicks may become more conspicuous as they approach fledging as a result of wing posturing behaviors and increased vo-

calization rates that could attract predators. We observed that chicks were often well hidden around the inside perimeter of retention fences or remained immobile under vegetation when we visited exclosures. However, in 2001 when we used less physical or vegetative cover, chicks moved continuously in the retention fence seeking escape cover, which increased their visibility to potential predators. We modified our techniques in 2002 by adding additional vegetation and/or artificial camouflage netting in and around retention fences, as well as releasing broods at earlier ages. Only one exclosed nest was depredated in 2002 suggesting our modifications were highly effective. However, placement of additional vegetation and camouflage in 2002 likely resulted in lower hatching success of exclosed nests relative to 2001. The third egg of a 3-egg clutch failed to hatch in three nests in 2002. We hypothesize the addition of dense vegetation within retention fences following hatch of the first two chicks impeded the view of the nesting adults and resulted in their failure to properly incubate the remaining egg. Adults may have only landed in exclosures to feed chicks or brood chicks for short periods. We recommend waiting several days after all chicks have hatched before gradually adding vegetation/camouflage to the retention fence over the course of several visits.

Chick Survival.—Nearly 90% of chicks survived in the absence of predation to 13–18 days in 2001–2002. We observed only six cases of mortality due to other causes and four of these were most likely influenced by investigator disturbance. These results suggest that predators were a primary cause of chick mortality in these wetlands and that weather, food resources, or disease were not significantly influencing chick survival at these sites in the 2 years studied. We cannot assess the magnitude of natural mortality due to predation without data on chick survival for unexclosed broods; however, the difficulty we had in preventing predation of broods attests to a significant level of predator activity in these wetlands. We could not identify the primary predators of chicks in this study. Many species occurring in Maine have been directly observed preying on Black Tern chicks and nests, or else have been implicated by indirect evidence in other studies: Great Blue Heron (*Ardea herodias*) (Chapman and Forbes 1984, Shealer and Haverland 2000), mink (*Mustela vison*) (Dunn 1979; Hickey 1997; F. A. Servello, pers. obs.), Northern Harrier (*Circus cyaneus*) (this study), Great Horned Owl (*Bubo virginianus*) (Bailey 1977, Einsweiller 1988), Black-crowned Night-heron (*Nycticorax nycticorax*) (Bailey 1977), common raccoon (*Procyon lotor*) (F. A. Servello, pers. obs.), Common Raven (*Corvus corax*) (this study), and fish (Don McDougal, pers. comm.).

Inadequate food provisioning was not a significant cause of chick mortality during the 2 years of study. Despite the presence of a size hierarchy within broods during the early posthatch period, differential growth (LGR and AM) with hatch order was not observed for either 2- or 3-chick broods. Furthermore, neither LGR nor AM decreased with increasing brood size, as would be expected if food provisioning was inadequate. Gilbert and Servello (2005) similarly found little evidence of food limitation during the 2 years prior to this study. Mean LGR and AM values for chicks were within ranges reported in other studies (Bailey 1977, Dunn 1979, Mosher 1986, Beintema 1997). Six chicks from three broods in 2001 had LGRs below 4.0 g/day and two of these chicks exhibited LGRs below the 3.32 g/day rate reported for starved Black Tern chicks in Europe (Beintema 1997). Four of these six chicks were depredated prior to release, one chick was found dead, apparently of starvation, and one chick was released. Two of these broods occurred in the same colony as broods exhibiting average to high LGRs suggesting factors other than food limitation may have been responsible for depressed growth. Starvation of chicks can be a direct result of insufficient food resources (poor foraging environment) or an indirect result of low "parental quality," whereby there is ample food but the parents do not provide sufficient food for their young (Nisbet et al. 1995).

Predator exclosures may be a useful conservation tool for increasing breeding productivity of small, high-risk populations of Black Terns. Our predator exclosures allowed adults to successfully raise broods of fledglings within a fenced structure and, therefore, we recommend the design as a research tool to obtain chick growth and survival data. Before

exclosures are implemented as a management tool, we recommend that Black Tern chick predators be identified regionally to assess if our exclosure design would be effective. Predator control (most commonly mammal trapping) has increased nest success for ducks (Sovada et al. 2001, Drever et al. 2004) and duckling survival (Pearse and Ratti 2004) in prairie pothole wetlands, but it is unclear if such control would be effective in Maine wetlands because the primary predators of Black Tern nests and chicks are not known. Predation should be considered a primary factor contributing to mortality of Black Tern chicks in Maine, and predation effects should be examined throughout the breeding range of the species to increase our understanding of factors limiting population growth.

ACKNOWLEDGMENTS

Funding or other support for this research was provided by the Maine Agricultural and Forest Experiment Station, U.S. Fish and Wildlife Service, Maine Outdoor Heritage Fund, Maine Department of Inland Fisheries and Wildlife, and Florida Power and Light—Maine Hydro. We thank Dan Noble, David Pert, S. K. Lemin, Sarah Case, and Nathan Poore for field assistance. Shannon Kearney and T. A. Gilbert were critical to the development of retaining fence and exclosure designs. We thank Mark McCollough and Don McDougal for valuable advice on our research and logistical support for fieldwork. We thank William Halteman and Raymond O'Connor for assistance with statistical analyses. We thank L. A. Hierl, T. J. Mabee, C. T. Collins, and C. E. Braun for useful reviews of this manuscript. This is Article Number 2952 of the Maine Agricultural and Forest Experiment Station.

LITERATURE CITED

Bailey, P. F. 1977. The breeding biology of the Black Tern (*Chlidonias niger surinamensis*). Thesis. University of Wisconsin, Oshkosh, USA.

Beintema, A. J. 1997. European Black Terns (*Chlidonias niger*) in trouble: examples of dietary problems. Colonial Waterbirds 20:558–565.

Bollinger, P. B. 1994. Relative effects of hatching order, egg-size variation, and parental quality on chick survival in Common Terns. Auk 111:263–273.

Bollinger, P. B., E. K. Bollinger, and R. A. Malecki. 1990. Tests of three hypotheses of hatching asynchrony in the Common Tern. Auk 107:696–706.

Brown, K. M. and R. D. Morris. 1996. From tragedy to triumph: renesting in Ring-billed Gulls. Auk 113:23–31.

Burger, J., I. C. T. Nisbet, C. Safina, and M. Gochfeld. 1996. Temporal patterns in reproductive success in the endangered Roseate Tern (*Sterna dougallii*) nesting on Long Island, New York, and Bird Island, Massachusetts. Auk 113:131–142.

Chapman, B. A. and L. S. Forbes. 1984. Observations on detrimental effects of Great Blue Herons on breeding Black Terns. Journal of Field Ornithology 55:251–252.

Cuthbert, F. J. and M. Y. Louis. 1993. The Forster's Tern in Minnesota: status, distribution, and reproductive success. Wilson Bulletin 105:184–187.

Cuthbert, N. L. 1954. A nesting study of the Black Tern in Michigan. Auk 71:36–63.

Drever, M. C., A. Wins-Purdy, T. D. Nudds, R. G. Clark, and D. A. Haukos. 2004. Decline in duck nest success revisited: relationships with predators and wetlands in dynamic prairie environments. Auk 121:497–508.

Dunn, E. H. 1979. Nesting biology and development of young in Ontario Black Terns. Canadian Field-Naturalist 93:276–281.

Dunn, E. H. and D. J. Agro. 1995. Black Tern (*Chlidonias niger*). The birds of North America. Number 147.

Einsweiller, S. S. 1988. Black Tern nesting biology in Cheboygan County, Michigan. Thesis. Central Michigan University, Mount Pleasant, USA.

Emms, S. K. and N. A. M. Verbeek. 1991. Brood size, food provisioning and chick growth in the Pigeon Guillemot *Cepphus columba*. Condor 93:943–951.

Estelle, V. B., T. J. Mabee, and A. H. Farmer. 1996. Effectiveness of predator exclosures for Pectoral Sandpiper nests in Alaska. Journal of Field Ornithology 67:447–452.

Eyler, T. B., R. M. Erwin, D. B. Stotts, and J. S. Hatfield. 1999. Aspects of hatching success and chick survival in Gull-billed Terns in coastal Virginia. Waterbirds 22:54–59.

Gilbert, T. A. and F. A. Servello. 2005. Insectivory versus piscivory in Black Terns: implications for food provisioning and growth of chicks. Waterbirds 28:436–444.

Hall, J. A. 1988. Early chick mobility and brood movements in the Forster's Tern (*Sterna forsteri*). Journal of Field Ornithology 59:247–251.

Hickey, J. M. 1997. Breeding biology and population dynamics of the Black Tern in western New York. Thesis. Cornell University, Ithaca, New York, USA.

Langham, N. P. E. 1972. Chick survival in terns (*Sterna* spp.) with particular reference to the Common Tern. Journal of Animal Ecology 41:385–396.

Larson, M. A., M. R. Ryan, and R. K. Murphy. 2002. Population viability of Piping Plovers: effects of predator exclusion. Journal of Wildlife Management 66:361–371.

Mabee, T. J. and V. B. Estelle. 2000. Assessing the effectiveness of predator exclosures for plovers. Wilson Bulletin 112:14–20.

Monaghan, P., J. D. Uttley, M. D. Burns, C. Thaine, and J. Blackwood. 1989. The relationship be-

tween food supply, reproductive effort and breeding success in the Arctic Tern *Sterna paradisaea*. Journal of Animal Ecology 58:261–274.

Morris, R. D., R. A. Hunter, and J. F. McElman. 1976. Factors affecting the reproductive success of Common Tern (*Sterna hirundo*) colonies on the lower Great Lakes during the summer of 1972. Canadian Journal of Zoology 54:1850–1862.

Mosher, B. 1986. Factors influencing reproductive success and nesting strategies in Black Terns. Dissertation. Simon Fraser University, Burnaby, British Columbia, Canada.

Nisbet, I. C. T., J. A. Spendelow, and J. S. Hatfield. 1995. Variations in growth of Roseate Tern chicks. Condor 97:335–344.

Nisbet, I. C. T., J. A. Spendelow, J. S. Hatfield, J. M. Zingo, and G. A. Gough. 1998. Variations in growth of Roseate Tern chicks. II. Early growth as an index of parental quality. Condor 100:305–315.

Pearse, A. T. and J. T. Ratti. 2004. Effects of predator removal on Mallard duckling survival. Journal of Wildlife Management 68:342–350.

Peterjohn, B. G. and J. R. Sauer. 1997. Population trends of Black Terns from the North American Breeding Bird Survey, 1996–1996. Colonial Waterbirds 20:566–573.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978–983.

Rimmer, D. W. and R. D. Deblinger. 1990. Use of predator exclosures to protect Piping Plover nests. Journal of Field Ornithology 61:217–223.

Robinson, J. A. and K. C. Hamer. 2000. Brood size and food provisioning in Common Terns *Sterna hirundo* and Arctic Terns *S. paradisaea*: consequences for chick growth. Ardea 88:51–60.

Safina, C., J. Burger, M. Gochfeld, and R. H. Wagner. 1988. Evidence for prey limitation of Common and Roseate tern reproduction. Condor 90: 852–859.

Servello, F. A. 2000. Population and research priorities for Black Terns developed from modeling analyses. Waterbirds 23:440–448.

Shealer, D. A. and J. A. Haverland. 2000. Effects of investigator disturbance on the reproductive behavior and success of Black Terns. Waterbirds 23: 15–23.

Shuford, W. D. 1999. Status assessment and conservation plan for the Black Tern (*Chlidonias niger surinamensis*) in North America. USDI, Fish and Wildlife Service, Denver, Colorado, USA.

Skagen, S. K. 1988. Asynchronous hatching and food limitation: a test of Lack's hypothesis. Auk 105: 78–88.

Sovada, M. A., R. M. Anthony, and B. D. J. Batt. 2001. Predation on waterfowl in arctic tundra and prairie breeding areas: a review. Wildlife Society Bulletin 29:6–15.

Starck, J. M. and R. E. Ricklefs. 1998. Avian growth and development: evolution within the altricial-precocial spectrum. Oxford University Press, Oxford, United Kingdom.

The Wilson Journal of Ornithology 120(1):176–180, 2008

USE OF CLAY LICKS BY MAROON-FRONTED PARROTS (*RHYNCHOPSITTA TERRISI*) IN NORTHERN MEXICO

RENE A. VALDÉS-PEÑA,[1,2] SONIA GABRIELA ORTIZ-MACIEL,[1] SIMON O. VALDEZ JUAREZ,[1] ERNESTO C. ENKERLIN HOEFLICH,[1] AND NOEL F. R. SNYDER[1]

ABSTRACT.—Geophagy has been documented in many species of birds, including many parrots, and its proposed functions include detoxification of dietary poisons, mineral supplementation, and acid buffering. Most geophagy reports involve tropical South American species; we present the first published report of clay-lick use by the Maroon-fronted Parrot (*Rhynchopsitta terrisi*), a species inhabiting high elevation temperate pine-oak (*Pinus* spp.–*Quercus* spp.) forest of the Sierra Madre Oriental. Thirty-six observation sessions were made at the four dispersed licks known from the restricted breeding range of this species. All known licks were near valley bottoms far below most nesting cliffs. Parrot visitations to ingest clay were characteristically in groups and the average number of parrots per group was nine individuals. Group visits averaged 18.3 min in duration and peaked between 0900 and 1100 hrs. The total number of parrots visiting licks during any day represented only a fraction of the known population of the species, suggesting that unless additional licks have yet to be discovered, visits of individuals to licks are relatively infrequent. *Received 18 September 2006. Accepted 22 May 2007.*

Geophagy is known primarily in herbivorous vertebrates including many ungulates, primates, elephants, reptiles, and a great diversity of birds (Emmons and Stark 1979, Jones and Hanson 1985, Izawa 1993). In birds, the trait has been described in cracids, corvids, pigeons, grouse, cassowaries, and hornbills (Prendergast and Boag 1970, Emmons and Stark 1979, Diamond et al. 1999), but is perhaps best known in parrots, where colorful aggregations of many species assemble at some of the earthen cliffs overlooking tributaries of the Amazon River. For example, hundreds of individuals of more than 20 parrot species are known to use licks overlooking the Tambopata River in the Tambopata-Candamo Reserve in Peru (Munn 1994, Brightsmith and Aramburú 2004). Other well known licks are in Manu National Park and along the Madre de Dios River of Peru (Gilardi et al. 1999); in Bolivia, >1,000 individuals of at least six species have been observed at a lick in the Valle de la Luna (Mee et al. 2005), while other licks occur in Amazonian regions of Colombia, Ecuador, and Brazil (Izawa 1993, Kyle 2001). Geophagy is also known for Grey Parrots (*Psittacus erithacus*) in the Congo Basin forest (May 2001) and a variety of Asian species in Papua, New Guinea (Diamond et al. 1999). Other observations of parrots eating soil have involved Lear's Macaws (*Anodorhynchus leari*) on their nest cliffs in eastern Brazil, Red-fronted Macaws (*Ara rubrogenys*) on their nest cliffs in Bolivia, and cockatoos ingesting soil in a city park in Australia (J. D. Gilardi, pers. comm.).

A variety of functions has been suggested for clay ingestion including gaining of mineral supplements, binding of toxic materials in diets, and regulation of pH in gut contents (Diamond et al. 1999, Gilardi et al. 1999). Studies by Gilardi et al. (1999) and Brightsmith and Aramburú (2004) in Peru suggest that both mineral supplementation and cytoprotection from secondary poisons in plant foods may be especially important functions.

Clay ingestion has not been well documented for parrots in Mexico. There have been observations suggesting ingestion of soil by Military Macaws (*Ara militaris*) in northeastern and southwestern Mexico (Juan Vargas and Carlos Bonilla, pers. comm.), and Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) and Lilac-crowned Parrots (*Amazona finschi*) in northwestern Mexico (Juan Vargas, pers. comm.). The trait was first clearly recognized in the Maroon-fronted Parrot (*Rhynchopsitta terrisi*) in 1995 at two mud-cliff sites still in use by the species today (NFRS). The objective of our study was to document basic features of clay-lick use by

[1] Centro de Calidad Ambiental, ITESM, CEDES 5ºpiso, Avenida, Eugenio Garza Sada 2501 sur CP 64849, Monterrey, N.L. México.

[2] Corresponding author; e-mail: ravp@itesm.mx

the Maroon-fronted Parrot during the breeding season, quantifying such features as group size, daily peaks in activity, and associated behaviors during clay ingestion.

METHODS

We observed four clay licks from June to September 2005 used by Maroon-fronted Parrots in 12, 3-day visits. All licks were in the Sierra Madre Oriental west and southwest of Monterrey, Nuevo Leon and were well distributed in the breeding range of the species in Nuevo Leon and Coahuila (Macias-Caballero 1998). Nesting of Maroon-fronted Parrots is mainly colonial and is only known to occur in natural cavities in vertical limestone cliffs. The parrots occur in this area only during the summer breeding season and migrate south in the Sierra Madre Oriental for the remainder of the year. We do not know if other licks occur in breeding and wintering areas of the species; however, coverage of the breeding area has been sufficiently intensive, especially through interviews of local residents, that we believe most licks in this region have been located. Two of the licks (Santa Cruz and Santa Rosa) are in Nuevo Leon. The other two (El Temporal and Ultimagua) are in Coahuila. Topographically, all four licks are close to valley bottoms in mud cliffs overlooking seasonal streams. None of the four licks is higher than 40 m above stream level and all are between 1,600 and 1,800 m above sea level. The most important nest cliffs of the species are at higher elevations (2,500–3,000 m above sea level).

The climate of the study area in the northern Sierra Madre Oriental corresponds to temperate subhumid forest with summer rains predominant. The annual temperature average is 14° C, with a range of 0 to 34° C. The average annual precipitation is 600 mm of which 370 mm occurs between June and September. The vegetation is predominantly pine-oak (*Pinus* spp.–*Quercus* spp.) forest. The Maroon-fronted Parrot primarily subsists on pine seeds of several species (mainly *Pinus cembroides*) with some use of acorns and agave seeds (Macias-Caballero et al. 1996). Much of this diet is considered to be chemically well defended with tannins (Wong 2007).

Clay licks were observed with binoculars and/or telescopes between 0700 (sunrise) and 1700 hrs (before sunset) from 50 to 100 m, depending on topography and availability of suitable viewing sites. We recorded the number of parrots arriving at the clay licks, time of arrival, time spent eating clay per flock, weather, and notes about their behavior and/or predator activity. We estimated the average number of parrots per flock that consumed clay and the average time these flocks were at clay licks.

RESULTS

Behavior.—Parrots usually arrived at clay licks in small groups (1–5 birds) giving typical flight vocalizations. The birds perched in nearby trees prior to landing at the clay cliffs, possibly assessing their surroundings for natural enemies. The first bird to land at the cliff was generally nervous in demeanor and normally did not begin feeding until joined closely by other parrots (within the next 2 min). During feeding, parrots flew to and from the lick regularly to change location on the cliff or to increase spacing with other parrots. We noted some parrots remained alert while others fed. The alert posture switched from one individual to another over time and, occasionally, the entire group on the cliff took flight simultaneously when one individual uttered a sharp alarm call. Feeding on soil typically occurred just below the top of the low cliffs, allowing the birds to quickly gain speed in leaving the cliffs by losing altitude. Sites used by parrots for ingesting clay showed the typical bird-created horizontal grooves, ledges, and hollows known for parrot clay licks in other regions and following particular soil horizons, which can be an indicator of preferred soils.

Periods of Clay Consumption.—Use of licks occurred throughout the day with the exception of the last 2 hrs in late afternoon (1500–1700 hrs). Use was greatest during morning and declined during the afternoon (Fig. 1). Peak use occurred in late morning (0900–1100 hrs), although at one lick the largest number of birds was observed between 0700 and 0900 hrs. The number of birds at another lick was equal between 0700–0900 and 0900–1100 hrs (Table 1).

Group Size and Number of Parrots at Licks.—Thirty-six groups of parrots were recorded in 12 days of observation with an average of three group visits per day for each of

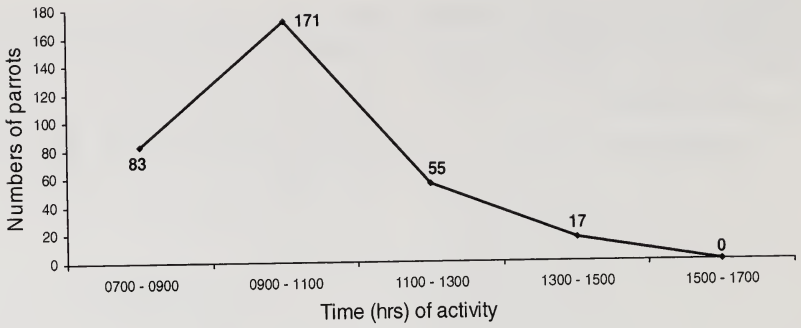


FIG. 1. Time of feeding (all observations) by Maroon-fronted Parrots at clay licks, Sierra Madre Oriental, Mexico (approx. sunrise at 0700 hrs and sunset at 1800 hrs).

the four clay licks (Table 1). The maximum simultaneous count of parrots at a lick was 28 and the maximum daily total for any lick was 63 individuals (in 5 groups). We recorded 326 birds eating clay and the average daily total was nine parrots per lick. These totals comprised only a small fraction of the estimated total parrot population (based on roost counts to be ~3,500 individuals at the time of the study).

Duration of Time at Licks.—Groups of parrots stayed on the cliffs from 1 to 52 min (Table 2) with an average of 18.3 min per group visitation. The averages are for groups and not for individuals, many of which spent significant amounts of time during feeding sessions in alert postures.

DISCUSSION

The Maroon-fronted Parrot exhibited a strong preference for use of clay licks in late morning (0900–1100 hrs) in contrast to the temporal use of licks by parrots in tropical America. The main use period at tropical American licks is during the first hour after dawn (Brightsmith 2004; Mee et al. 2005; J. D. Gilardi, pers. comm.). Large macaws and some parakeets have their main activity in late morning and afternoons (Brightsmith 2004). Maroon-fronted Parrots also visit licks in early morning, but the emphasis on late morning visitations suggests clay ingestion followed first feedings.

We are unsure if additional clay licks exist in the Maroon-fronted Parrot range. However, interviews of local residents and knowledge that all known licks were in low-elevation sites of relatively easy access, suggest the four known licks could represent all licks in use by the parrot population or at least those they most used and frequented. This possibility is also suggested by the dispersed distribution of the licks relative to known nesting colonies of the species. Twenty-one nesting colonies are presently known for the species (Macias-Caballero 1998) and the greatest distance from known colonies to the nearest lick is 17.5 km. This distance compares with distances of 16 km estimated for parrots flying to and from licks in Peru (Brightsmith 2004). Ortiz-Maciel (2000) estimated individual Maroon-fronted Parrots flew as far as 23 km from breeding colonies and the known distribution

TABLE 1. Numbers of Maroon-fronted Parrots at clay licks in the Sierra Madre Oriental, Mexico.

	Numbers of parrots								
Time (hrs)	Sta. Cruz	Sta. Rosa	Temporal	Ultimagua	Totals	Range	$\bar{x}$	± SD	Groups (*n*)
0700–0900	6	44	8	25	83	2–16	8.3	±4.4	10
0900–1100	42	34	70	25	171	2–28	11.4	±7.8	15
1100–1300	21	22	0	12	55	1–8	7.8	±5.8	7
1300–1500	4	10	3	0	17	3–6	4.2	±1.2	4
1500–1700	0	0	0	0	0	0	0	0	0
Totals	73	110	81	62	326	1–28	9	±6.4	36

TABLE 2. Time (min) of Maroon-fronted Parrots at clay licks, Sierra Madre Oriental, Mexico.

		Time at clay licks (min)		
Clay lick	Groups (*n*)	Range	$\bar{x}$	± SD
Sta. Cruz	8	1–49	21.1	± 15.89
Sta. Rosa	15	1–52	15.6	± 12.05
Temporal	7	9–31	19.1	± 8.15
Ultimagua	6	5–48	20.3	± 17.85
Totals	36	1–52	18.3	± 13.27

of clay licks could serve all known breeding colonies without need for additional licks.

The two largest known Maroon-fronted Parrot colonies, comprising about 83% of the breeding population (in 2005), are 15.5 and 9.25 km from the nearest licks, and separated from the licks by 1,200 m elevation. The cost of flying to and from licks may cause parrots to delay visits to licks until late morning after their first feedings. Ortiz-Maciel (2000) indicated that peak morning movements of Maroon-fronted Parrots occurred between 0600 and 0900 hrs.

The relatively low numbers of parrots visiting licks on any day strongly suggests that individual parrots may visit licks infrequently. Visits of the species to favored water sites for drinking, at times attracts up to 1,000 individuals per day (NFRS). Observations of the closely-related Thick-billed Parrot (Snyder et al. 1999) suggest daily drinking periods for individuals—a dramatic contrast to the apparent low frequency of clay ingestion in Maroon-fronted Parrots.

Maroon-fronted Parrot groups at licks averaged nine individuals and spent an average of 18.3 min at the licks. In South America, where many parrot species use the same licks and group sizes are often much larger, the average time individuals spent at licks ranged from 28.7 to 47.4 min for diverse species (Burger and Gochfeld 2003). The behavior of individual Maroon-fronted Parrots at licks was generally similar to that described for other species.

Given the average of three groups per day with nine birds at each clay lick (108 birds), we hypothesize parrots use the lick once every 2.7 days based on a breeding population of ~300 birds in 2005. This hypothesis should be tested with uniquely marked parrots to obtain a more accurate average and the extent of individual variation in visitation rates.

Maroon-fronted Parrots have a diet of pine seeds and acorns which is rich in protein, carbohydrates, and fiber (Fonseca 2003). Wong (2007) found that pinion seeds (mainly *Pinus cembroides*) eaten by Maroon-fronted Parrots had low levels of Na, Ca, Mn, and S; these minerals occurred in high levels in consumed clay. Wong (2007) also found that clay had minerals such as kaolin, smectite, and micas that can absorb secondary compounds such as polyphenols and alkaloids suggesting the clays could also buffer acids. These findings suggest that parrots consume clay to help in absorption of dietary toxins, mineral supplements, and acid buffering capacity as also demonstrated by Gilardi et al. (1999).

We recommend that areas used for geophagy be included as important sites for conservation of Maroon-fronted Parrots and that future studies of their ecology continue to document geophagy activity by including more visits to the clay licks. Future activities should involve local people to implement ecotourism in these areas.

ACKNOWLEDGMENTS

We thank the team work of the Centro de Calidad Ambiental at ITESM *Campus* Monterrey, without them this work could not have happened. Their friendship and desire to work for conservation of psitacids contributed to our success. We also thank Jamie Gilardi, Eduardo Iñigo, and Donald Brightsmith for comments and revision of this paper, and CONACYT, and the National Commission of Natural Protected Areas of Mexico (CONANP) for financial support. We also thank all the volunteers that collaborated in field work and the local people whose hospitality made our field stays especially pleasant.

LITERATURE CITED

Brightsmith, D. J. 2004. Effects of weather on avian geophagy in Tambopata, Peru. Wilson Bulletin 116:134–145.

Brightsmith, D. J. and R. Aramburú. 2004. Avian geophagy and soil characteristics in southeastern Peru. Biotropica 36:534–543.

Burger, J. and M. Gochfeld. 2003. Parrot behavior at a Rio Manu (Peru) clay lick: temporal patterns, associations, and antipredator responses. Acta Ethologica 6:23–34.

Diamond, J., K. D. Bishop, and J. D. Gilardi. 1999. Geophagy in New Guinea birds. Ibis 141:181–193.

Emmons, L. and N. M. Stark. 1979. Elemental com-

position of a natural mineral lick in Amazonia. Biotropica 11:311–313.

Fonseca, J. R. M. 2003. De piñas y piñones. Ciencias 69:64–65.

Gilardi, J. D., S. S. Duffey, C. A. Munn, and L. A. Tell. 1999. Biochemical functions of geophagy in parrots: detoxification of dietary toxins and cytoprotective effects. Journal of Chemical Ecology 25:897–922.

Izawa, K. 1993. Soil-eating by alouatta and ateles. International Journal of Primatology 14:229–242.

Jones, R. L. and H. C. Hanson. 1985. Mineral licks, geophagy and biogeochemistry of North American ungulates. Iowa State University Press, Ames, USA.

Kyle, T. 2001. Geophagy in the Amazon: mammalian and avian utilization of clay licks in Amazonian Peru. Thesis. Frostburg State University, Frostburg, Maryland, USA.

Macias-Caballero, C. M. 1998. Comportamiento de anidación y monitoreo de la productividad de las colonias de la cotorra serrana oriental (*Rhynchopsitta terrisi*) en el Norte de México. Thesis. Instituto Tecnologico y de Estudios Superiores de Monterrey, Monterrey, Mexico.

Macias-Caballero, C. M., E. C. Enkerlin-Hoeflich, N. F. R. Snyder, and A. Garza L. 1996. ¡Vamos por buen camino! Estudio y conservación de las cotorras serranas orientales. DUMAC 18:28–34.

May, D. L. 2001. Grey Parrots of the Congo Basin forest. Psittascene 47:8–10.

Mee, A., R. Denny, K. Fairclough, D. M. Pullan, and W. Boyd-Wallis. 2005. Observations of parrots at a geophagy site in Bolivia. Biota Neotropica 5:321–324.

Munn, C. A. 1994. Macaws: winged rainbows. National Geographic 185:118–140.

Ortiz-Maciel, S. G. 2000. Uso del paisaje por la Cotorra Serrana Oriental (*Rhynchopsitta terrisi*). Thesis. Instituto Tecnologico y de Estudios Superiores de Monterrey, Monterrey, Mexico.

Prendergast, B. A. and D. A. Boag. 1970. Seasonal changes in the diet of Spruce Grouse in central Alberta. Journal of Wildlife Management 34:605–611.

Snyder, N. F. R., E. C. Enkerlin-Hoeflich, and M. A. Cruz-Nieto. 1999. Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*). The birds of North America. Number 406.

Wong, K. 2007. Funciones bioquímicas de la geofagia en la Cotorra Serrana Oriental (*Rhynchopsitta terrisi*). Thesis. Instituto Tecnologico y de Estudios Superiores de Monterrey, Monterrey, Mexico.

The Wilson Journal of Ornithology 120(1):181–189, 2008

CAVITY NUMBER AND USE BY OTHER SPECIES AS CORRELATES OF GROUP SIZE IN RED-COCKADED WOODPECKERS

JOHN J. KAPPES JR.[1,2]

ABSTRACT.—I examined cavity number and use by other species as correlates of Red-cockaded Woodpecker (*Picoides borealis*) group size at Camp Blanding Training Site (CBTS) and Goethe State Forest (GSF), Florida. Group size was positively correlated with cavity number at CBTS but not at GSF. Other species occupied 1.75 (34%) and 1.19 (27%) cavities/territory at CBTS and GSF, respectively. Statistically controlling for use by other species yielded significant positive correlations between group size and cavity number in 4 of 5 years at CBTS and 2 of 4 years at GSF. Correlations between group size and total use by other species, controlling cavity number, were significantly negative at both sites. Separating total use by species, group size was negatively correlated only with southern flying squirrels (*Glaucomys volans*) at CBTS and only with Red-bellied Woodpeckers (*Melanerpes carolinus*) at GSF, as flying squirrels occupied >3 times more cavities/territory at CBTS than at GSF (0.87 vs. 0.28) while Red-bellied Woodpeckers occupied ~0.75 cavities/territory at both sites. Flying squirrels may obscure the relationship between the two woodpecker species by limiting their cavity use.
Received 10 January 2006. Accepted 28 June 2006.

Woodpeckers (Picidae) and other excavators are generally less cavity-limited than nonexcavating cavity nesters (Wesolowski 1983, Martin 1993). The quality of an excavator territory (as defined by survival and reproductive success) is a function of the number of suitable cavities and depletion of this resource by other species (Kilham 1961, Short 1979, Kerpez and Smith 1990, Li and Martin 1991, Ingold 1994, Sedgwick 1997, Kappes 2004). Cavity availability may limit the size and fitness of family groups in the case of cooperatively breeding cavity nesters (Ligon and Ligon 1990).

The Red-cockaded Woodpecker (*Picoides borealis*) is a federally endangered cooperative breeder endemic to fire-maintained pine (*Pinus* spp.) forests of the southeastern United States. Family groups consist of one breeding pair and 0–3 helpers, and reproductive success and individual survival increases with group size (Walters 1990, Khan and Walters 2002, USDI 2003). The availability of cavities, which are excavated in living pines and used for nesting and year-round for roosting, is the primary factor affecting territory quality (Ligon 1970, Copeyon et al. 1991, Walters et al. 1992, Davenport et al. 2000). Cavities require one to many years to excavate but often remain suitable for a decade or longer, even after periods of abandonment or use by other species (Conner and Rudolph 1995, Harding and Walters 2002). Sets of cavity trees, termed clusters (Walters 1990), are typically aggregated within a group's territory. The most recently completed cavity usually becomes the breeding male's roost (Conner et al. 1998) and the group's nest cavity (Ligon 1970). Breeding females, helpers, and juveniles roost individually in older cavities, including former nest holes, and may be more prone to mortality or dispersal in cavity-limited territories (Carter et al. 1989, Doerr et al. 1989, Carrie et al. 1998, Daniels and Walters 2000, Kappes 2004). Thus, group stability and size can be cavity limited (Copeyon et al. 1991, Carrie et al. 1998).

Cavities of Red-cockaded Woodpeckers are commonly usurped and/or pre-emptively occupied by other cavity-nesting species (Kappes 1997, 2004). Research on the impact of these interactions on Red-cockaded Woodpeckers has focused on the effects of one species, southern flying squirrels (*Glaucomys volans*) (hereafter flying squirrels), on the reproductive success of groups of Red-cockaded Woodpeckers containing at least a breeding pair (Conner et al. 1996, Laves and Loeb 1996, Mitchell et al. 1999). I monitored Red-cockaded Woodpecker group size, cavity number, and rate of cavity use by other spe-

[1] Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA.

[2] Current address: Department of Biological Sciences, Virginia Tech, Blacksburg, VA 24061, USA; e-mail: kappes@vt.edu

cies at two forests from 1997 to 2001. I used correlative analyses to evaluate the hypotheses that: (1) cavity number may limit group size, and (2) cavity occupation by other species can cause or exacerbate this limitation by reducing cavity availability.

Group size is defined as the number of territory occupants, including "groups" of 0 and 1. This definition allows evaluation of the response of group size across a broader range of territory quality (as measured by cavity availability), including territories where cavity availability is too low to support a breeding pair. I predicted that clusters with low cavity availability (few suitable cavities and/or high use by other species) are more likely to be unoccupied (group size = 0), or occupied by single males (group size = 1). Clusters with intermediate levels of cavity availability are more likely to support an unassisted pair (group size = 2). Territories with relatively high cavity availability (high number of cavities and/or low use by other species) are more likely to have pairs with helpers (group size ≥3).

METHODS

Study Area.—The study was conducted at two forests in northern peninsular Florida: Camp Blanding Training Site (CBTS) (81° 58′ N, 29° 59′ W) in Clay County and Goethe State Forest (GSF) (82° 38′ N, 29° 16′ W) in Levy County, where ~16 (Kappes et al. 2004) and 30 groups of Red-cockaded Woodpeckers occurred, respectively. All cavity-tree clusters were in open, mature longleaf pine (*Pinus palustris*) forest with an understory dominated by saw palmetto (*Serenoa repens*) and wiregrass (*Aristida stricta*). Prescribed fires were conducted at 3–5 year intervals. Fieldwork consisted of monitoring Red-cockaded Woodpecker group size, cavity number, and cavity occupancy. I monitored 14 clusters at CBTS in 1997, 13 clusters in 1998 and 1999, and 16 clusters in 2000 and 2001 (total = 72 cluster years). I monitored 15 clusters at GSF in 1998 and 17 clusters from 1999 to 2001 (total = 66 cluster years). I only monitored suitable cavities within these clusters, as defined by entrance diameter ≤60 mm, an intact floor, and occurrence in a living tree (Rudolph et al. 1990b, Kappes and Harris 1995). All study clusters included at least three suitable cavities and were surrounded by sufficient foraging habitat to support a group of Red-cockaded Woodpeckers (USDI 2003).

Cavity Monitoring.—Cavity clusters were censused 7–9 times per breeding season (Apr–Jul) at 10–14 day intervals using diurnal and nocturnal inspections, and roost checks. I initially inspected each cavity in each census interval during the day using either ladders, a droplight and a mirror, or a video camera mounted on a telescoping pole (TreeTop Peeper, Sandpiper Technologies Inc., Manteca, CA, USA). I inspected the bole of each cavity tree to ascertain the status of the resin barrier, which is maintained by Red-cockaded Woodpeckers on currently used cavity trees to deter rat snakes (*Elaphe* spp.) (Jackson 1974, Rudolph et al. 1990a). If a cavity was empty, but exhibited abundant evidence of fresh resin-barrier maintenance (clear sap exuding from resin-wells excavated by the woodpecker), I assumed it was occupied by Red-cockaded Woodpeckers in that census interval (Jackson 1977). This assumption was confirmed with an evening (pre-sunset) roost check in which the cavity was watched from an unobtrusive distance to ascertain if any birds entered it to roost. In most cases, multiple cavities were observed during a single roost check. If, during the daytime census, the cavity contained flying squirrels, a nocturnal species that dens in cavities during the day, I recorded that species as the occupant (flying squirrels enter den cavities before woodpeckers exit their roost cavities, and vice versa, precluding any temporal partitioning of cavity occupancy). If avian eggs or nestlings, or some other taxon were found, I recorded the appropriate species as the occupant at that census. If a cavity was empty during the daytime inspection and exhibited marginal evidence of resin-barrier maintenance, or if its resin-barrier status had changed since the previous census, it was revisited for an evening roost check. Empty cavities exhibiting no evidence of current resin-barrier maintenance were included in an evening roost check, or re-inspected after dark for roosting birds using an infrared option on a video camera. I calculated the mean number of cavities occupied by each species for each cluster as the average across the 7–9 censuses. A species' *occupancy* or *cavity use* was the mean number of Red-cockaded Woodpecker

cavities in a cluster year that were occupied by that species. *Cavities* refer specifically to being suitable for Red-cockaded Woodpeckers.

Data Analysis.—I only used data from 1998 to 2001 to compare the composition of the animal communities occupying cavities at the two study sites as data from 1997 were lacking for GSF. Correlation analysis was used to evaluate the relationships between group size and (1) cavity number, (2) use by Red-bellied Woodpeckers (*Melanerpes carolinus*), (3) use by flying squirrels, and (4) total use by other species. The variables were rarely normally distributed because of small annual sample sizes or inherent skewness of the data and transformations failed to remedy this problem. I used Spearman's rank methods, with few exceptions, to calculate simple (bivariate) and partial correlations (Shipley 2000). One-tailed tests were used based on *a priori* predictions that group size would increase with increasing cavity number and decrease with increasing levels of occupancy by other species. *P* values ≤0.03 were considered strongly significant, *P* values >0.03 but ≤0.05 were considered significant, and *P* values >0.05 but <0.10 were considered marginally significant.

RESULTS

Community Compositions.—The annual means (a mean of means) of group size of Red-cockaded Woodpeckers at CBTS and GSF were 2.26 (range = 2.13–2.46) and 2.31 (range = 2.18–2.41), respectively (Fig. 1A). The annual mean number of suitable cavities per cluster was 5.13 (range = 4.88–5.46) at CBTS and 4.35 (range = 4.20–4.47) at GSF. Mean group size was similar at the two forests, but the mean number of cavities was consistently higher at CBTS (Fig. 1A).

Annual mean occupancy by Red-bellied Woodpeckers was 0.73 (range = 0.63–0.82) cavities per cluster at CBTS and 0.77 (range = 0.66–0.84) at GSF (Fig. 1B). Annual mean occupancy by flying squirrels at CBTS and GSF were 0.87 (range = 0.6–1.03) and 0.28 (range = 0.15–0.38) cavities per cluster, respectively. The annual mean number of cavities per cluster occupied by passerines (Great Crested Flycatcher [*Myiarchus crinitus*], Tufted Titmouse [*Baeolophus bicolor*], and Eastern Bluebirds [*Sialia sialis*]) was similar at the

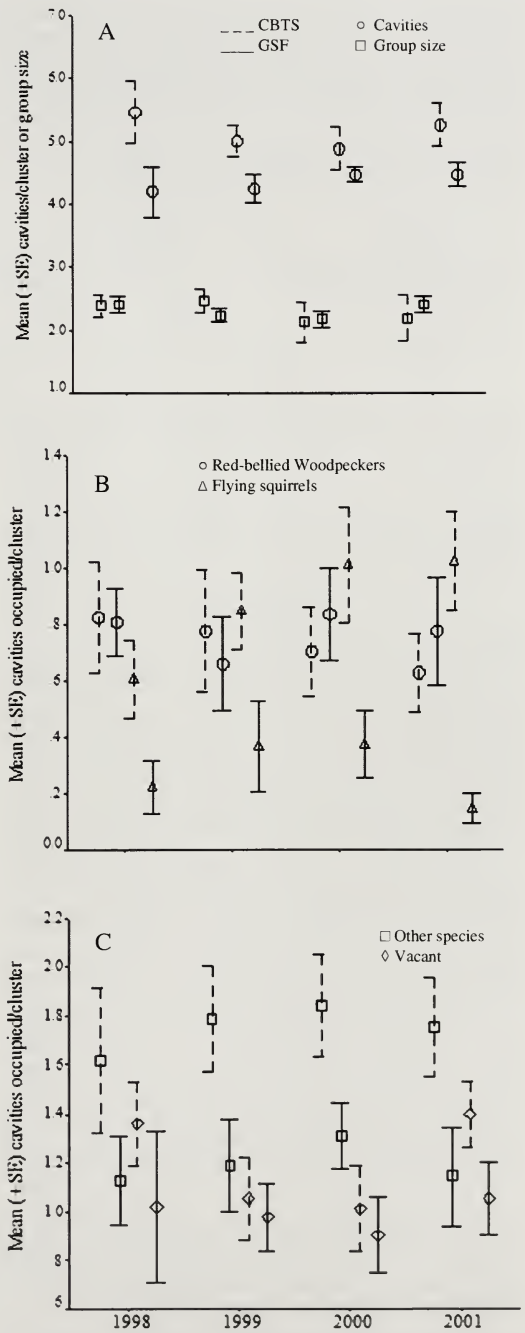


FIG. 1. (A) Red-cockaded Woodpecker group size and number of suitable cavities per cluster, (B) mean number of suitable Red-cockaded Woodpecker cavities per cluster occupied by Red-bellied Woodpeckers and southern flying squirrels, and (C) mean number of suitable Red-cockaded Woodpecker cavities per cluster occupied by other species and mean number of vacant cavities per cluster. Camp Blanding Training Site (CBTS; dashed error bars) and Goethe State Forest (GSF; solid error bars), 1998–2001.

TABLE 1. Coefficients of variation for annual mean use of Red-cockaded Woodpecker cavities by Red-bellied Woodpeckers, southern flying squirrels, and all other species (i.e., including Red-bellied Woodpeckers and southern flying squirrels) combined, Camp Blanding Training Site (CBTS; $n = 5$ years) and Goethe State Forest (GSF; $n = 4$ years), Florida.

Species	CBTS	GSF
Red-bellied Woodpecker	0.116	0.099
Southern Flying Squirrel	0.223	0.401
All other species	0.054	0.070

two sites, averaging 0.10 (range = 0.05–0.13) cavities per cluster at CBTS and 0.12 (range = 0.07–0.17) at GSF. Total cavity use by other species (i.e., other than Red-cockaded Woodpeckers) averaged 1.75 (range = 1.62–1.84) cavities per cluster at CBTS and 1.19 (range = 1.12–1.31) at GSF (Fig. 1C). The mean number of vacant cavities per cluster was similar at the two sites (Fig. 1C).

Cavity use by Red-bellied Woodpeckers was similar at the two sites, as was cavity use by passerines, but use by flying squirrels was 3.11 times greater (range = 2.3–6.9 across years) at CBTS than at GSF. Total cavity use by other species was 1.47 times greater (range = 1.40–1.53) at CBTS than at GSF due to greater use by flying squirrels (Fig. 1C). Total use by other species at both sites exhibited less annual variation than either Red-bellied Woodpeckers or flying squirrels (Table 1).

Correlations Between Group Size and Measures of Cavity Availability.—Correlations between group size and cavity number at CBTS were positive but non-significant from 1997 to 1999, and strongly significant in 2000 and 2001 (Table 2). No relationship was detected at GSF (Table 2). Raw cavity numbers underestimated availability because of high rates of use by other species. I calculated partial correlations between group size and cavity number, controlling for use by other species. This substantially increased the correlation at CBTS; the relationship became strongly significant in all years except 1999 (Table 2). The strength of the relationship increased in all years at GSF, becoming strongly significant in 1998 and marginally significant in 2000 (Table 2).

Correlations Between Group Size and Cavity Use by Other Species.—Variation in cavity number affected the relationship between group size and cavity use by other species. Thus, I calculated the partial correlations, controlling for cavity number. The partial correlations between group size and cavity use by Red-bellied Woodpeckers indicated no consistent association between these variables at CBTS (Table 3). The partial correlations between cavity use by flying squirrels and group size were consistently negative, being marginally significant in 1997 and 2000, and strongly significant in 1999 and 2001. Partial correlations between group size and total cavity use by other species at CBTS revealed a strongly significant negative relationship in all years except 1999 (Table 3).

The partial correlations between group size and cavity use by Red-bellied Woodpeckers were negative at GSF, being significant in 1998 and strongly significant in 1999 (Table 3). No relationship between group size and cavity use by flying squirrels was evident at GSF. The partial correlations between group size and total cavity use by other species were consistently negative, being strongly signifi-

TABLE 2. Spearman's rank correlations and partial Spearman's rank correlations (controlling for use by other species) between Red-cockaded Woodpecker group size and cavity number, Camp Blanding Training Site (CBTS) and Goethe State Forest (GSF), Florida.

Forest	1997	1998	1999	2000	2001
Simple correlations					
CBTS	0.279	0.179	0.363	0.514***[a]	0.558***
GSF	No data	0.335	0.000	0.121	0.000
Partial correlations					
CBTS	0.655***[a]	0.624***	0.027	0.681***	0.786***
GSF	No data	0.627***	0.253	0.411*	0.143

[a] One-tailed test, *$0.10 > P > 0.05$, ***$P < 0.03$.

TABLE 3. Spearman's rank partial correlations, controlling for cavity number, between Red-cockaded Woodpecker group size and mean number of cavities used by Red-bellied Woodpeckers, southern flying squirrels, and all other species (i.e., including Red-bellied Woodpeckers and southern flying squirrels) combined, Camp Blanding Training Site (CBTS) and Goethe State Forest (GSF), Florida.

Species	1997	1998	1999	2000	2001
CBTS					
Red-bellied Woodpecker	−0.391*[a]	−0.317	0.504**	0.034	0.042
Southern Flying Squirrel	−0.421*	−0.270	−0.695***	−0.414*	−0.676***
All other species	−0.619***	−0.632***	0.231	−0.529***	−0.673***
GSF					
Red-bellied Woodpecker	No data	−0.472**[b]	−0.722***	−0.138	−0.310[b]
Southern Flying Squirrel	No data	−0.299	0.016	−0.308	0.222
All other species	No data	−0.615***	−0.437**	−0.564***	−0.231

[a] One-tailed test, *$0.10 > P > 0.05$, **$0.05 > P > 0.03$, ***$P < 0.03$.
[b] Pearson's partial correlation.

cant in 1998 and 2000, and significant in 1999 (Table 3).

Potential Higher Order Interactions.—The partial correlations between group size and total cavity use by other species were consistently and significantly negative at both forests, whereas those between group size and individual species differed between forests (Table 3). I hypothesized the relationship between group size and cavity use by Red-bellied Woodpeckers changed between forests because of the inter-forest difference in cavity use by flying squirrels. I evaluated this hypothesis by calculating partial correlations between group size and cavity use by Red-bellied Woodpeckers, controlling for both cavity number and use by flying squirrels. I predicted these correlations would be more negative than those controlling only for cavity number. Further, the negative relationship should increase more at CBTS where cavity use by flying squirrels was greater. The results supported these predictions (Table 4). The correlations at CBTS became strongly significant in 1997 and marginally significant in 2000 and 2001. The correlations at GSF remained relatively unchanged, increasing only in 2000 (Table 4).

DISCUSSION

My primary hypotheses were: (1) Red-cockaded Woodpecker group size is cavity-limited, and (2) use of cavities by other species can cause or exacerbate this limitation. The data support these hypotheses indicating that group size is limited by cavity availability, as estimated by accounting for resource use by other species.

The primary species causing the negative relationship between group size and total cavity use by other species changed between forests with level of use by flying squirrels (Table 3, Fig. 1B), suggesting complex relationships among the three species studied. Where cavity use by flying squirrels was relatively high (CBTS), it limited both group size and cavity use by Red-bellied Woodpeckers, obscuring the relationship between the two species of woodpeckers. The negative effect of Red-bellied Woodpeckers on group size was manifested only where cavity use by flying squirrels was low (GSF) or statistically controlled

TABLE 4. Spearman's rank partial correlations between Red-cockaded Woodpecker group size and number of cavities used by Red-bellied Woodpeckers, controlling for both southern flying squirrel use and cavity number, Camp Blanding Training Site (CBTS) and Goethe State Forest (GSF), Florida.

Forest	1997	1998	1999	2000	2001
CBTS	−0.602***[a]	−0.338	−0.006	−0.391*	−0.378*
GSF	No data	−0.409*	−0.741***	−0.547***	−0.214

[a] One-tailed test, *$0.10 > P > 0.05$, ***$P < 0.03$.

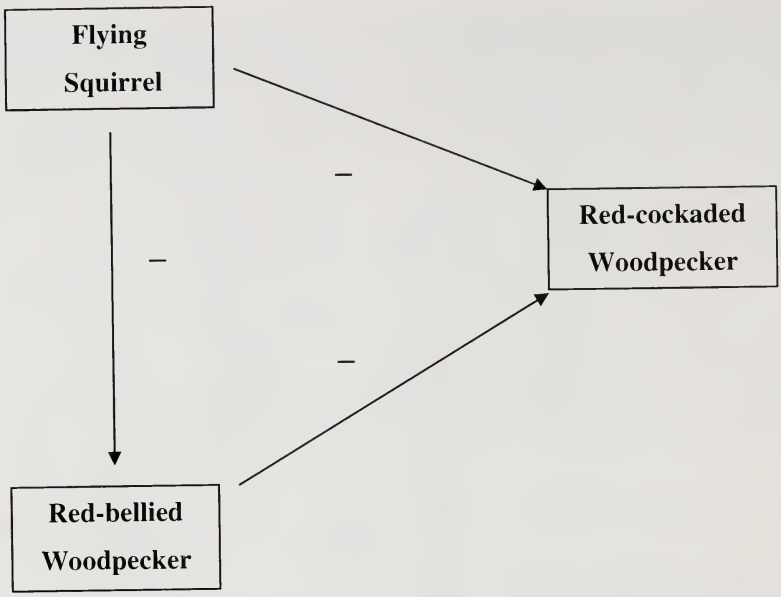


FIG. 2. Community interaction web for Red-cockaded Woodpeckers, southern flying squirrels, and Red-bellied Woodpeckers. Arrows point from the dominant to subdominant species for each direct, negative (–) interaction illustrating a transitive dominance hierarchy.

(CBTS). Flying squirrels may impart a positive indirect effect on group size by limiting cavity use by Red-bellied Woodpeckers (an interaction chain; Wootton 1994) in addition to its direct negative effect on group size (Lawlor 1979; Fig. 2). The management practice of removing flying squirrels from cavities (Mitchell et al. 1999, USDI 2003) may competitively release Red-bellied Woodpeckers, which may preempt a response by Red-cockaded Woodpeckers.

Further evidence of a consequential interaction between flying squirrels and Red-bellied Woodpeckers is that annual variation in mean occupancy by each of these species was greater than annual variation in total cavity use by other species (Table 1, Fig. 1B, C). This pattern might result from compensation in cavity use by Red-bellied Woodpeckers in response to variation in use by flying squirrels. I evaluated this explanation by calculating the correlation between the annual mean cavity use of Red-bellied Woodpeckers and that of flying squirrels using data from CBTS, where both species were well represented, and found a strongly negative relationship (r_s = 0.900, P = 0.037, n = 5 years).

The correlations between group-size and other variables were weaker at GSF than at CBTS (Tables 2–4). Lower group size variation (within years) at GSF compared to CBTS may have contributed to this pattern (Fig. 1A). Over 98% of the cluster years at GSF involved groups composed of 2–3 individuals. Seventy-six percent of the cluster years at CBTS involved groups of 2–3 individuals, 15% involved 0–1 individual, and 8% involved 4–5 individuals. Another possible explanation for the weaker correlations at GSF was a greater rate of cavity tree mortality in that forest compared to CBTS (0.29 cavity trees/cluster/year vs. 0.04 cavity trees/cluster/year; J. J. Kappes, unpubl. data). This relatively high rate of cavity tree mortality at GSF may have precluded group size from tracking cavity availability because Red-cockaded Woodpeckers typically abandon cavity trees that die (Ligon 1970) as a resin barrier can no longer be maintained.

Unmeasured components of territory quality likely influenced group size at both forests. The most important of these factors is recurrent fire, which improves the quality of foraging habitat, thereby enhancing group formation, stability, reproductive success, and size (James et al. 1997, Walters et al. 2002,

USDI 2003, Kappes et al. 2004). Members of groups in high-quality foraging habitat may be in better physical condition enabling them to better survive bouts of roosting outside (Williams et al. 1991), thereby bolstering group size even in cavity-limited clusters.

Certain aspects of the ecology of Red-cockaded Woodpeckers may predispose this species to cavity limitation and exacerbation of this limitation by other species. The slow supply rate of cavities is often exceeded by rates of loss to tree mortality, cavity enlargement, and usurpation by other species, resulting in cavity shortages (Conner et al. 2001, Harding and Walters 2002). Moreover, because recurrent fire in this ecosystem often maintains low densities of snags, which are used by other excavators as cavity sites (Ligon 1970, Kappes and Harris 1995), cavities used by Red-cockaded Woodpeckers constitute a disproportionate number of sites available to other cavity nesters, intensifying interactions at these sites.

Caution is warranted in inferring a causal relationship between cavity use by other species and group size. Support for alternative explanations for the correlations, however, is lacking. That larger groups might be better at defending roost cavities from potential usurpers is doubtful because each group member defends only its own roost (Davis et al. 2005). Also, other species would be less likely to limit group size if they primarily occupied surplus cavities. However, cavity usurpation by other species was common, demonstrating these species regularly used cavities that would otherwise be used by Red-cockaded Woodpeckers. A Markov model analysis of cavity use data indicates the probabilities of transition in cavity use (over the 10–14 day census intervals), from Red-cockaded Woodpeckers to Red-bellied Woodpeckers and from Red-cockaded Woodpeckers to flying squirrels were 0.014 and 0.015, respectively at CBTS and 0.013 and 0.002, respectively at GSF (JJK, unpubl. data). Most of these transitions were due to direct displacement. The methods used in this study did not quantify outside roosting by Red-cockaded Woodpeckers, but displaced birds were observed roosting outside or in lower quality cavities while other species occupied apparently suitable back-up sites. Cavity usurpation by other species was the sole cause of frequent outside roosting by adult Red-cockaded Woodpeckers in another north Florida study in which outside roosting could be quantified (Kappes 1993, 1997).

This and previous work suggests that both Red-bellied Woodpeckers and flying squirrels are dominant over Red-cockaded Woodpeckers in cavity-associated interactions, supporting the conclusion the negative correlation between group size and other species was caused by the latter. The Red-bellied Woodpecker has been commonly observed physically displacing Red-cockaded Woodpeckers from roost cavities (Ligon 1970, Baker 1971, Jackson 1978, Kappes 1997, this study), whereas observations of the reverse are rare (J. H. Carter, unpubl. data; JJK, unpubl. data). Interactions between flying squirrels and Red-cockaded Woodpeckers are rarely observed because they apparently occur at night. Repeated observations of flying squirrels occupying active cavities of Red-cockaded Woodpeckers, while evicted birds roost outside or in lower quality cavities, indicate that flying squirrels often displace this woodpecker (Loeb 1993; JJK, unpubl. data). If Red-cockaded Woodpeckers displaced flying squirrels with any regularity, this should have been observed during the hundreds of pre-sunset roost checks conducted during this study, but no such displacement was observed. Apparent transitions from flying squirrels to Red-cockaded Woodpeckers were often recorded, but most of these likely involved undetected intermediate transitions from flying squirrels to vacancy, which result from the habit of this species for moving frequently among multiple den cavities within their territories (Bendel and Gates 1987) or from predation by rat snakes (Kappes 2004). Removal experiments will be required to further evaluate the hypothesis that cavity occupation by other species can limit group size of Red-cockaded Woodpeckers.

ACKNOWLEDGMENTS

J. M. Davis, John Mahan, Michael Meisenberg, D. I. Stanish, J. A. Surdick, Diana Swan, Melissa Warren, and M. I. Williams assisted with fieldwork. The Florida Army National Guard, Camp Blanding Training Site; Goethe State Forest; and the U.S. Fish and Wildlife Service, Clemson Field Office provided funding, study sites, and logistical support. K. E. Sieving, Ralph Costa, R. T. Engstrom, M. D. Moulton, C. W. Osenberg, R. R. Schaefer, C. E. Braun, four anonymous

reviewers, and the J. R. Walters Laboratory at Virginia Tech (J. R. Walters, L. A. Blanc, B. J. Olsen, J. M. Johnson, and J. L. Perkins) provided useful comments on earlier drafts.

LITERATURE CITED

Baker, W. W. 1971. Progress report on life history studies of the Red-cockaded Woodpecker at Tall Timbers Research Station. Pages 44–59 *in* Ecology and management of the Red-cockaded Woodpecker (R. L. Thompson, Editor). USDI, Fish and Wildlife Service and Tall Timbers Research Station, Tallahassee, Florida, USA.

Bendel, P. R. and J. E. Gates. 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). Journal of Mammalogy 68:243–255.

Carrie, N. R., K. R. Moore, S. A. Stephens, and E. L. Keith. 1998. Influence of cavity availability on Red-cockaded Woodpecker group size. Wilson Bulletin 110:93–99.

Carter III, J. H., J. R. Walters, S. H. Everhart, and P. D. Doerr. 1989. Restrictors for Red-cockaded Woodpecker cavities. Wildlife Society Bulletin 17:68–72.

Conner, R. N. and D. C. Rudolph. 1995. Excavation dynamics and use patterns of Red-cockaded Woodpecker cavities: relationships with cooperative breeding. Pages 343–352 *in* Red-cockaded Woodpecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Editors). College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. The Red-cockaded Woodpecker: surviving in a fire-maintained ecosystem. University of Texas Press, Austin, USA.

Conner, R. N., D. C. Rudolph, D. Saenz, and R. R. Schaefer. 1996. Red-cockaded Woodpecker nesting success, forest structure, and southern flying squirrels in Texas. Wilson Bulletin 108:697–711.

Conner, R. N., D. Saenz, D. C. Rudolph, W. G. Ross, and D. L. Kulhavy. 1998. Red-cockaded Woodpecker nest-cavity selection: relationships with cavity age and resin production. Auk 115:447–454.

Copeyon, C. K., J. R. Walters, and J. H. Carter III. 1991. Induction of Red-cockaded Woodpecker group formation by artificial cavity construction. Journal of Wildlife Management 55:549–556.

Daniels, S. J. and J. R. Walters. 2000. Between-year breeding dispersal in Red-cockaded Woodpeckers: multiple causes and estimated cost. Ecology 81: 2473–2484.

Davenport, D. E., R. A. Lancia, J. R. Walters, and P. D. Doerr. 2000. Red-cockaded Woodpeckers: a relationship between reproductive fitness and habitat in the North Carolina Sandhills. Wildlife Society Bulletin 28:426–434.

Davis, J. M., K. E. Sieving, and J. J. Kappes Jr. 2005. Red-cockaded Woodpecker roost cavity defense during the non-breeding season. Florida Field Naturalist 33:81–92.

Doerr, P. D., J. R. Walters, and J. H. Carter III. 1989. Reoccupation of abandoned clusters of cavity trees (colonies) by Red-cockaded Woodpeckers. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 43:326–336.

Harding, S. R. and J. R. Walters. 2002. Processes regulating the population dynamics of Red-cockaded Woodpecker cavities. Journal of Wildlife Management 66:1083–1095.

Ingold, D. J. 1994. Influence of nest-site competition between European Starlings and woodpeckers. Wilson Bulletin 106:227–241.

Jackson, J. A. 1974. Gray rat snakes versus Red-cockaded Woodpeckers: predator-prey adaptations. Auk 91:342–347.

Jackson, J. A. 1977. Determination of the status of Red-cockaded Woodpecker colonies. Journal of Wildlife Management 41:448–452.

Jackson, J. A. 1978. Competition for cavities and Red-cockaded Woodpecker management. Pages 103–112 *in* Endangered birds: management techniques for the preservation of threatened species (S. A. Temple, Editor). University of Wisconsin Press, Madison, USA.

James, F. C., C. H. Hess, and D. Kufrin. 1997. Species-centered environmental analysis: indirect effects of fire history on Red-cockaded Woodpeckers. Ecological Applications 7:118–129.

Kappes, J. J. 1993. Interspecific interactions associated with Red-cockaded Woodpecker cavities at a north Florida site. Thesis. University of Florida, Gainesville, USA.

Kappes, J. J. 1997. Defining cavity-associated interactions between Red-cockaded Woodpeckers and other cavity-dependent species: interspecific competition or cavity kleptoparasitism? Auk 114:778–780.

Kappes, J. J. 2004. Community interactions associated with Red-cockaded Woodpecker cavities. Pages 458–467 *in* Red-cockaded Woodpecker: road to recovery (R. Costa and S. J. Daniels, Editors). Hancock House Publishers, Blaine, Washington, USA.

Kappes, J. J. and L. D. Harris. 1995. Interspecific competition for Red-cockaded Woodpecker cavities in Apalachicola National Forest. Pages 458–467 *in* Red-cockaded Woodpecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Editors). College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Kappes, J. J., K. E. Sieving, J. Davis, M. D. Adams, J. Garrison, P. Catlett, M. Corby, and R. Costa. 2004. Status and management of Red-cockaded Woodpeckers at Camp Blanding Training Site, Florida. Pages 198–202 *in* Red-cockaded Woodpecker: road to recovery (R. Costa and S. J.

Daniels, Editors). Hancock House Publishers, Blaine, Washington, USA.

Kerpez, T. A. and N. S. Smith. 1990. Competition between European Starlings and native woodpeckers for nest cavities in saguaros. Auk 107:367–375.

Khan, M. Z. and J. R. Walters. 2002. Effects of helpers on breeder survival in the Red-cockaded woodpecker (*Picoides borealis*). Behavioral Ecology and Sociobiology 51:336–344.

Kilham, L. 1961. Reproductive behavior of Red-bellied Woodpeckers. Wilson Bulletin 73:237–255.

Laves, K. S. and S. C. Loeb. 1996. Effects of southern flying squirrels (*Glaucomys volans*) on Red-cockaded Woodpecker (*Picoides borealis*) reproductive success. Animal Conservation 2:295–303.

Lawlor, L. R. 1979. Direct and indirect effects of *n*-species competition. Oecologia 43:355–364.

Li, P. and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

Ligon, J. D. 1970. Behavior and breeding biology of the Red-cockaded Woodpecker. Auk 87:255–278.

Ligon, J. D. and S. H. Ligon. 1990. Green Woodhoopoes: life history traits and sociality. Pages 33–65 *in* Cooperative breeding in birds: long term studies of ecology and behavior (P. B. Stacey and W. D. Koenig, Editors). Cambridge University Press, Cambridge, United Kingdom.

Loeb, S. C. 1993. Use and selection of Red-cockaded Woodpecker cavities by southern flying squirrels. Journal of Wildlife Management 57:329–335.

Martin, T. E. 1993. Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities? American Naturalist 142:937–946.

Mitchell, L. R., L. D. Carlile, and C. R. Chandler. 1999. Effects of southern flying squirrels on nest success of Red-cockaded Woodpeckers. Journal of Wildlife Management 63:538–545.

Rudolph, D. C., R. N. Conner, and J. Turner. 1990a. Competition for Red-cockaded Woodpecker roost and nest cavities: effects of resin age and entrance diameter. Wilson Bulletin 102:23–36.

Rudolph, D. C., H. Kyle, and R. N. Conner. 1990b. Red-cockaded Woodpeckers versus rat snakes: the effectiveness of the resin barrier. Wilson Bulletin 102:14–22.

Sedgwick, J. A. 1997. Sequential cavity use in a cottonwood bottomland. Condor 99:880–887.

Shipley, B. 2000. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge, United Kingdom.

Short, L. L. 1979. Burdens of the picid hole-excavating habit. Wilson Bulletin 91:16–28.

U.S. Department of Interior (USDI). 2003. Recovery plan for the Red-cockaded Woodpecker (*Picoides borealis*): second revision. USDI, Fish and Wildlife Service, Atlanta, Georgia, USA.

Walters, J. R. 1990. The Red-cockaded Woodpecker: a "primitive" cooperative breeder. Pages 67–101 *in* Cooperative breeding in birds: long term studies of ecology and behavior (P. B. Stacey and W. D. Koenig, Editors). Cambridge University Press, Cambridge, United Kingdom.

Walters, J. R., C. K. Copeyon, and J. H. Carter III. 1992. Test of the ecological basis of cooperative breeding in Red-cockaded Woodpeckers. Auk 109:90–97.

Walters, J. R., S. J. Daniels, J. H. Carter, and P. D. Doerr. 2002. Defining quality of Red-cockaded Woodpecker foraging habitat based on habitat use and fitness. Journal of Wildlife Management 66:1064–1082.

Wesolowski, T. 1983. Conjectures, venturous suggestions or 'evolution of hole-nesting in birds'? Ornis Scandinavica 14:63–65.

Williams, J. B., M. A. Du Plessis, and W. R. Siegfried. 1991. Green Woodhoopoes (*Phoeniculus purpureus*) and obligate cavity roosting provide a test of the thermoregulatory insufficiency hypothesis. Auk 108:285–293.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25:443–466.

Short Communications

The Wilson Journal of Ornithology 120(1):190–195, 2008

First Description of Nests and Eggs of Two Hispaniolan Endemic Species: Western Chat-tanager (*Calyptophilus tertius*) and Hispaniolan Highland-tanager (*Xenoligea montana*)

Christopher C. Rimmer,[1,6,7] Lance G. Woolaver,[2] Rina K. Nichols,[2] Eladio M. Fernández,[3] Steven C. Latta,[4] and Esteban Garrido[5]

ABSTRACT.—We present the first nest descriptions for two Hispaniolan endemic songbirds, the Western Chat-tanager (*Calyptophilus tertius*) and Hispaniolan Highland-tanager (*Xenoligea montana*) from a montane broadleaf forest site in the Sierra de Bahoruco of the Dominican Republic. Single Western Chat-tanager nests were found on 17 May 2002 and 9 June 2004. Both were coarsely-built, partially-domed, bulky structures 1.0–1.5 m above ground. One nest was freshly-depredated when found, whereas the second contained two eggs which hatched on 19 and 20 June. The nestlings were depredated on 25 June. A Hispaniolan Highland-tanager nest found on 27 June 2004 fledged a single chick the following day. This nest, in a vine tangle 2.5 m above ground, was an open cup structure composed of moss, small herbaceous stems, leaf fragments, lichens, and other plant fibers. We describe the eggs of both species, the nestlings of Western Chat-tanager, and the juvenal plumage of Hispaniolan Highland-tanager. We believe that depredation by introduced feral cats (*Felis domesticus*) and rats (*Rattus* spp.) is a serious problem in these montane forests. *Received 26 December 2006. Accepted 16 April 2007.*

Hispaniola supports more endemic bird species than any other Caribbean island, but the breeding biology of its avifauna remains poorly known. Breeding bird communities in the island's high elevation broadleaf and mixed pine-broadleaf forests have received little study because of the remoteness and difficulty of access of these forests. We documented previously undescribed nests of two species during investigations at a montane forest site in the Dominican Republic during 2002–2004. The Western Chat-tanager (*Calyptophilus tertius*) and Hispaniolan Highland-tanager (*Xenoligea montana*) are among the most endangered species on Hispaniola; understanding their breeding biology is fundamental to conserving their populations.

The Western Chat-tanager, recently classified as a species distinct from the Eastern Chat-tanager (*Calyptophilus frugivorus*) (AOU 1998), occupies a disjunct and fragmented range at elevations from 750 to 2,300 m in Haiti's Massif de la Hotte and Massif de la Selle, and in the western Sierra de Bahoruco of the Dominican Republic (Latta et al. 2006). The species inhabits dense understory of moist broadleaf forests where it is secretive and difficult to observe. The International Union for the Conservation of Nature (IUCN) has not recognized the recent split of *C. tertius* from *C. frugivorus*, but still considers the species complex as globally Vulnerable to extinction because of its small range and overall population size (IUCN 2006). Data on abundance and population trends are lacking, but there is little doubt that declines have occurred because of habitat loss throughout Hispaniola (Keith et al. 2003, Latta et al. 2006). Two formerly recognized subspecies are believed to have been extirpated (IUCN 2006).

The Hispaniolan Highland-tanager, also known as the White-winged Warbler (AOU 1998), is restricted in Haiti to mesic montane forest above 1,150 m elevation in the Massif de la Hotte of Haiti. This species was renamed

[1] Vermont Institute of Natural Science, 6565 Woodstock Road, Quechee, VT 05059, USA.

[2] Wildlife Preservation Canada, 5420 Highway 6 North, Guelph, ON N1H 6J2, Canada.

[3] Sociedad Ornitológica de la Hispaniola, Avenue, Máximo Gómez, esq. San Martín, Edificio Fundación Progressio, Tercero Piso, Santo Domingo, República Dominicana.

[4] National Aviary, Allegheny Commons West, Pittsburgh, PA 15212, USA.

[5] Grupo Jaragua, Inc., Calle El Vergel 33, El Vergel, Santo Domingo, República Dominicana.

[6] Current address: Vermont Center for Ecostudies, P. O. Box 420, Norwich, VT 05055, USA.

[7] Corresponding author; e-mail: crimmer@vinsweb.org

by Latta et al. (2006) based on mtDNA analyses showing this species' clear association with the tanagers of Hispaniola (Lovette and Bermingham 2002). It has apparently been extirpated from the Massif de la Selle and other areas of former occurrence. The species' Dominican Republic distribution is limited to elevations above 1,300 m in Sierra de Bahoruco, parts of the Cordillera Central, and on upper slopes of the southern Sierra de Neiba (Latta et al. 2006). The Hispaniolan Highland-tanager is classified as globally Vulnerable by the IUCN (2006) and is considered by some to be one of Hispaniola's most endangered endemic birds (Woods et al. 1992, Latta et al. 2006). No data exist on population size or trends, but local extirpations and ongoing severe deforestation suggest the species is in decline.

The objectives of this paper are to describe: (1) the nest and eggs of Western Chat-tanager and Hispaniolan Highland-tanager, (2) the natal plumage of Western Chat-Tanager, and (3) the juvenal plumage of Hispaniolan Highland-tanager.

METHODS

We conducted studies of the breeding bird community at a montane broadleaf forest site at Pueblo Viejo (18° 12′ N, 71° 32′ W) at 1,775 m elevation in the Sierra de Bahoruco from May through July 2002–2004. General floristic features of this forest type have been described by Fisher-Meerow and Judd (1989) and Latta et al. (2003). Nest searching was conducted on a daily basis each year, primarily through systematic searching of suitable habitat. We fitted five Western Chat-tanagers with 1.0-g radio transmitters (BD-2 model, Holohil Systems Ltd., Carp, ON, Canada) in 2002 and 2003 and tracked each individual daily to attempt to locate nests. Once located, nests of all species were monitored at 2–3-day intervals through termination (failure or fledging); some nest visits occurred at 1-day intervals. We measured a standardized series of habitat and nest site characteristics following each nesting attempt.

NEST DESCRIPTION

Western Chat-tanager.—CCR found a nest on 17 May 2002 by systematically searching an area in which a radio-marked female and male had been present during the previous several days. The nest was 1.3 m above ground in an extremely dense vine-shrub thicket in a tree-fall gap and could be accessed only by crawling on the ground. It was on top of the horizontal "roof" of the vine tangle, under the small overhanging branch of a 2.5-m tall broadleaf shrub that projected above the undergrowth. Estimated percent nest concealment from 1 m was 20% above, 90% below, 70% north, 80% east, 10% south, and 0% west. Fresh eggshell fragments, as well as the continued nearby presence of both female and male Chat-tanagers suggested the nest had been recently depredated and it was collected at this time.

The nest was a bulky, coarsely-constructed, partially-domed structure with a west-facing side entrance that covered two-thirds of the nest cup. The exterior consisted of small woody stems 2–4.5 mm in diameter, robust herbaceous stems, peeled coarse exterior sheathing of herbaceous stems, vine tendrils, moss, and foliose lichens. About 40% of the outer layer was covered with the entire leaves of at least three broadleaf tree or shrub species. The inner cup was lined primarily with fine herbaceous stems and leaf fragments. The exterior diameter from back to the bottom rim of the entrance was 21.5 cm, from back to the entrance's top rim 14.5 cm, and from side to side 23.5 cm. The nest cup measured 13.1 cm from front to back, 11.1 cm from side to side, and 5.1 cm from back to the top edge of the entrance. The overall nest height was 13.1 cm.

A second nest of this species was discovered on 9 June 2004 by RKN and LGW when an adult flushed from close range. The nest was in a small clearing (~5 m diameter) within dense, mature broadleaf forest, 3 m from an actively-used foot trail. The nest was 1.1 m above ground on the eastern side of the lower trunk of a hardwood "ozua" (*Pimenta ozua*) tree. The nest tree was 13 m tall with its lower canopy 7.5 m above ground and a diameter at breast height of 19.7 cm. The nest was against the trunk and supported beneath by a collection of vines with two main stems (4.0 and 3.0 mm diameter) interwoven with the top of the nest, two main stems on the bottom of the nest (10.0 and 5.0 mm diameter), and several smaller stems 0.3–1.0 mm in diameter touching the side of the nest. Estimated vegetation concealment

FIG. 1. Western Chat-tanager nest with eggs, June 2004. Photograph by L. G. Woolaver.

for the nest from a distance of 1 m was 0% overhead, 90% below, 95% north, 10% east, 20% south, and 85% west. This cover was provided by the tree trunk and surrounding tangle of vine stems.

This nest also was a large, bulky structure, roughly oval in shape (Fig. 1). The nest cup was partially covered by a roof, creating a south-facing entrance 8.7 cm high and 8.2 cm wide. The exterior was composed of moss and lichens interwoven with twigs and whole herbaceous stalks from 1 to 5.5 mm diameter, stripped sheathing of herbaceous stems, dried leaf fragments of broadleaf species, and fragments of dried bromeliad leaves. The inner cup was lined with fine twigs and herbaceous stems, dried leaf fragments, lichen, moss, and a few adult body feathers. The exterior nest dimensions were 28.5 cm from front to back, 27.0 cm from side to side, and 26.0 cm from top to bottom. The nest cup measured 9.1 cm from front to back, 7.7 cm from side to side, and 5.5 cm in depth. The nest cup height from the roof to the bottom was 14.3 cm.

The nest contained two eggs when discovered on 9 June. The eggs had pale blue background coloration and irregular light brown to dark brown speckling and mottling (Fig. 1). The eggs measured 27.8 × 18.7 and 28.9 × 18.8 mm and hatched on 19 and 20 June, respectively. No eggshells were found in the nest, suggesting the adults had removed them. The nestlings were dark pink with whitish bills and gapes, and covered with long, fine, black down. The nestlings were last confirmed alive at 1515 hrs EST on 25 June and both were missing from the nest at 0558 hrs on 26 June. The nest was damaged, suggesting depredation and it was collected on this date.

Observations on adult behavior at this nest were recorded by EMF from a photographic blind during 5 hrs on 20 June, shortly after the eggs hatched. The smaller of the two adults was banded and presumed to be the female, based

FIG. 2. Hispaniolan Highland-tanager nest with egg, June 2004. Photograph by E. M. Fernández.

on brooding behavior. The nestlings were brooded for 10–16 min periods each hour during which the female faced the nest entrance. The male fed the female a small white grub during one brooding session and provided her with small arthropods on several occasions while she was foraging near the nest. Both adults fed the chicks, but the male's feeding visits were infrequent and sporadic. The female fed the nestlings at 15–20-min intervals when not brooding. Each feeding bout consisted of 4–5 consecutive flights to the nest during which the female approached using a consistent pattern of perches. Her vocalizations changed from a short, two note "*chip-chip*" while foraging to an even "*tick, tick, tick, tick . . .*" as she approached the nest. The female was twice observed removing fecal pellets from the nest, although it was unclear whether she ate these or carried them away. The male sang for 10–15 min bouts each hour from different perches, but within 10 m of the nest.

Hispaniolan Highland-tanager.—Pablo Díaz found a nest of this species on 27 June 2004 containing one egg and one nestling that appeared close to fledging. The nest was in a dense vine tangle 2.5 m above ground. The vine thicket reached a height of 4.5 m and was in the understory of a closed-canopy broadleaf forest. Estimated percent nest cover from 1 m was 70% overhead, 70% north, 20% east, 60% south, and 70% west.

The nest was an open, cup-shaped structure (Fig. 2). The nest's exterior was composed of moss, small herbaceous stems, broadleaf leaf fragments, lichens, and other plant fibers. Its exterior cup was lined with fine, hairlike plant fibers and small numbers of herbaceous stems <1 mm in diameter. The exterior nest diameter was 10.5×7.9 cm, the nest cup diameter

was 5.6 × 5.2 cm, and the interior depth was 3.1 cm. The nest height was 5.5 cm. The single egg was oval in shape, pale greenish-white in background coloration, and faintly marked with reddish brown blotches and scrawls (Fig. 2). No measurements were obtained and the egg subsequently disappeared. The nestling fledged on 28 June.

The juvenal plumage, previously undescribed, was documented through photographs taken by EMF. The head and nape were brownish-gray, whereas the remaining upperparts were grayish tinged with olive-brown. The emerging flight feathers appeared dark grayish, the secondaries were edged greenish orange-brown proximally, and the greater coverts were predominantly greenish orange-brown. The underparts were a smudgy off-white with some brownish tones. The bill was grayish-flesh, the legs pale grayish, and the eye dark brownish.

DISCUSSION

Confirmed descriptions of the nests of the Western Chat-tanager or Hispaniolan Highland-tanager have not been published prior to this paper. Bond (1943:122) reported a possible Chat-tanager nest from the Massif de la Selle range in Haiti: "A single nest, containing one addled egg (23.6 × 18.3 mm) . . . , probably pertained to this species. This nest (found on June 14) was situated in a fern about two feet above the ground, bordering a blackberry patch. There was a protesting pair of Chat Tanagers a few yards from the nest . . . ". The timing of this discovery and the egg dimensions are similar to our data, but more substantive information is lacking.

Two descriptions of apparent Hispaniolan Highland-tanager nests from the early 1900s are less convincing. One was shown to Bond (1928) on 11 June 1928 from Morne La Selle in Haiti. Wetmore and Swales (1931:396) described the nest as "globular in shape, composed of moss and grasses, lined with grass stems and feathers, and placed in a bush five feet from the ground." It contained "two fresh eggs, which are plain, creamy white in color without markings". Bond (1928) reported the respective egg measurements as 21.6 × 15.5 and 21.7 × 15.5 mm. The second reputed nest was reported to Wetmore and Swales (1931: 397) by local residents at an unspecified location, and described as "oval with the entrance from beneath". It is unlikely that either of these two nests was that of a Hispaniolan Highland-tanager, based on our documentation of the Pueblo Viejo nest.

Our limited observations suggest the peak incubation period for Western Chat-tanagers occurs from mid-May to mid-June. Further evidence of this species' nesting phenology is provided by two mist-netted females with fully-developed incubation or brood patches. One was captured on 16 May 2002 and the second on 18 May 2003 (CCR, unpubl. data). Both encounters indicate that incubation was underway by mid-May. The Hispaniolan Highland-tanager fledging date of 27 June is later than the mean (± SD) fledging date of 1 June ± 25.5 days for the ecologically similar Green-tailed Ground-tanager (*Microligea palustris*) at Pueblo Viejo (n = 14 nests; CCR and SCL, unpubl. data), but well within the range of expected variation.

The depredation of both Western Chat-tanager nests highlights the generally high rates (~50%) of nest predation in montane broadleaf forests of the Sierra de Bahoruco. Introduced predators, particularly feral cats (*Felis domesticus*), black (*Rattus rattus*) and Norway rats (*R. norvegicus*), appear to limit nest success of several endemic montane species, especially those which forage and nest near the ground. The remains of the 2004 Western Chat-tanager nest do not allow us to identify the predator(s), as the nest had been pulled from below and the bottom ripped apart, leading us to believe a mammal was responsible.

High elevation broadleaf forests are considered one of Hispaniola's most endangered habitats (Latta and Lorenzo 2000). Ten of the 15 endemic bird species considered endangered or threatened on the island are concentrated in montane forests (Latta et al. 2006). Understanding factors that limit populations of these species is crucial to implementing successful management and conservation practices. Our documentation of the first nests of Western Chat-tanager and Hispaniolan Highland-tanager contributes to an emerging base of information on the ecology of these two species, both of which are regarded at high risk of extinction.

ACKNOWLEDGMENTS

We thank Jesus Almonte, Nicolas Corona, Pablo Díaz, J. D. Lambert, Danilo Mejía, Vinicio Mejía, Marisabel Paulino, Andrea Townsend, and Jason Townsend for assistance with very challenging field work. Funding was provided by the Bay Foundation, National Geographic Society, Scott Neotropical Fund of the Lincoln Park Zoo, Wildlife Preservation Canada, and friends of the Vermont Institute of Natural Science. Authorization to conduct our work was provided by the Subsecretaría de Areas Protegidas and Departamento de Vida Silvestre, Dominican Republic. Constructive reviews of the manuscript were provided by W. J. Arendt and J. W. Wiley.

LITERATURE CITED

American Ornithologists' Union (AOU). 1998. Checklist of North American birds. Seventh Edition. American Ornithologists' Union. Washington, D.C., USA.

Bond, J. 1928. The distribution and habits of the birds of the Republic of Haiti. Proceedings of the Academy of Natural Sciences of Philadelphia 80:483–521.

Bond, J. 1943. Nidification of the passerine birds of Hispaniola. Wilson Bulletin 55:115–125.

Fisher-Meerow, L. L. and W. S. Judd. 1989. A floristic study of five sites along an elevational transect in the Sierra de Bahoruco, Prov. Pedernales, Dominican Republic. Moscosoa 5:159–185.

International Union for the Conservation of Nature (IUCN). 2006. 2006 IUCN Red List of threatened species. ⟨www.iucnredlist.org⟩.

Keith, A. R., J. W. Wiley, S. C. Latta, and J. A. Ottenwalder. 2003. The birds of Hispaniola—Haiti and the Dominican Republic. BOU Checklist 21. British Ornithologists' Union, Tring, United Kingdom.

Latta, S. C. and R. Lorenzo (Editors). 2000. Results of the national planning workshop for avian conservation in the Dominican Republic. Dirección Nacional de Parques, Santo Domingo, Dominican Republic.

Latta, S. C., C. C. Rimmer, and K. P. McFarland. 2003. Winter bird communities in four habitats along an elevational gradient on Hispaniola. Condor 105:179–197.

Latta, S., C. Rimmer, A. Keith, J. Wiley, H. Raffaele, K. McFarland, and E. Fernandez. 2006. Birds of the Dominican Republic and Haiti. Princeton University Press, Princeton, New Jersey, USA.

Lovette, I. J. and E. Bermingham. 2002. What is a wood-warbler? Molecular characterization of a monophyletic Parulidae. Auk 119:695–714.

Wetmore, A. and B. H. Swales. 1931. Birds of Haiti and the Dominican Republic. U.S. National Museum Bulletin 155.

Woods, C. A., F. E. Sergile, and J. A. Ottenwalder. 1992. Stewardship plan for the national parks and natural areas of Haiti. Florida Museum of Natural History, Gainesville, USA.

The Wilson Journal of Ornithology 120(1):195–199, 2008

Foraging and Nesting of the 'Akikiki or Kaua'i Creeper (*Oreomystis bairdi*)

Eric A. VanderWerf[1,3,4] and Pauline K. Roberts[2]

ABSTRACT.—The 'Akikiki or Kaua'i Creeper (*Oreomystis bairdi*) is a rare, little-known Hawaiian honeycreeper endemic to the island of Kaua'i. Its range is contracting, the population is declining, and it is a candidate for listing under the U.S. Endangered Species Act. We report an instance of foraging by excavation observed on 22 May 2006, a behavior previously unknown in this species, and on parental behavior at two nests observed on 24 May 2006 and 27 May 2007, about which there is little previous information. Both parents brought food to the nest, the male provided food for the female, and the female also foraged independently. The nesting pair in 2007 had a juvenile from a previous nest, indicating the 'Akikiki will attempt to raise two broods. These observations are of limited extent, but even small facts can contribute to our understanding of the biology of the 'Akikiki and causes of its decline. *Received 1 February 2007. Accepted 16 June 2007.*

[1] U.S. Fish and Wildlife Service, 300 Ala Moana Boulevard, Room 3-122, Box 50088, Honolulu, HI 96850, USA.

[2] Kaua'i Forest Bird Recovery Project, Hawai'i Division of Forestry and Wildlife, P. O. Box 458, Waimea, HI 96796, USA.

[3] Current address: Pacific Rim Conservation, 3038 Oahu Avenue, Honolulu, HI 96822, USA.

[4] Corresponding author; e-mail: ewerf@hawaii.rr.com

The ʻAkikiki or Kauaʻi Creeper (*Oreomystis bairdi*) is a small forest bird in the Hawaiian honeycreeper subfamily (Drepanidinae: Fringillidae) endemic to the island of Kauaʻi. It was once found throughout Kauaʻi and was locally abundant in the Alakaʻi and Kokeʻe areas into the early 1960s (Richardson and Bowles 1964). It has disappeared from much of the island and is now restricted to high elevation native forests in remote parts of the Alakaʻi Plateau (USFWS 1984, Scott et al. 1986, Foster et al. 2004). Forest bird surveys have shown a decrease in distribution from 88 to 36 km^2 between 1970 and 2000 and a decline in estimated population from 6,832 ± 966 to 1,472 ± 680 birds over this period (Foster et al. 2004).

No field research has focused on the ʻAkikiki and we assume the causes of this decline are those typical of other Hawaiian forest birds: diseases carried by non-native mosquitoes, degradation of native forest habitat by invasive non-native plants, browsing and rooting by feral ungulates, and nest predation by non-native rodents (Foster et al. 2000, Scott et al. 2001, USFWS 2006). The threat from mosquito-borne diseases may worsen as global warming allows mosquitoes to invade the highest, coldest parts of the island that once provided a refuge from disease (Benning et al. 2002). The ʻAkikiki has been a candidate for listing under the U.S. Endangered Species Act since 1994 due to its small and declining population, restricted distribution, and a variety of threats (USFWS 2004). It is considered critically endangered by the International Union for the Conservation of Nature (IUCN 2006).

The ʻAkikiki is one the least-known of all extant Hawaiian bird species. Only eight ʻAkikiki nests are known and there is no information about nest success, parental care of nestlings, reproductive rates, survival of adults or juveniles, or movements (Eddinger 1972, Foster et al. 2000, USFWS 2006).

The objective of this paper is to report observations on foraging and nesting of the ʻAkikiki from trips to the Alakaʻi Wilderness Preserve from 22 to 24 May 2006 and 24 to 28 May 2007. The primary purpose of these trips was to conduct forest bird surveys and research on the critically-endangered Puaiohi or small Kauaʻi Thrush (*Myadestes palmeri*). These observations on the ʻAkikiki are of limited extent, but even small facts can contribute to our understanding of the biology of this species and causes of its decline.

OBSERVATIONS

On 22 May 2006, EAV observed a pair of ʻAkikiki foraging in the forest canopy on a low ridge in the upper Halepaʻakai drainage. The birds visited several trees and spent ~1 min foraging on branches and twigs of a small, partly dead ʻōlapa (*Cheirodendron trigynum*) tree. They appeared to be gleaning and probing for insects on the bark, but photographs of one of the birds revealed that it had also been excavating rotten wood from the center of a twig, presumably for insect larvae (Fig. 1). The freshly excavated area where the bird had been working could be identified by the pale color of the newly exposed wood. Two small pieces of wood were visible on the bird's bill. There also were areas of darker, more weathered wood on the same twig that appeared to be older excavations.

We discovered an ʻAkikiki nest on 24 May 2006, ~12.5 m above ground level in a 14 m tall ʻōhiʻa (*Metrosideros polymorpha*) tree on a bank of Halepaʻakai Stream. Our attention was drawn to the tree by songs and calls from the male and by the unusual amount of time spent in the tree by the pair. The nest was positioned in a fork where several epiphyte-encrusted branches ~1–3 cm in diameter diverged from a larger branch (Fig. 2). The composition of the nest could not be examined closely due to its height, but it appeared to be composed of moss, small pieces of bark, bits of lichen, and fine plant fibers (Fig. 2).

We observed the nest from 1045 to 1215 hrs HST and made notes about all activity. One individual, assumed to be the female based on its behavior, sat on the nest continuously and left the nest once for 20 min. The head of one nestling was visible just over the rim of the nest (Fig. 2). A second adult, assumed to be the male, fed the female twice on the nest and the female passed food to the nestling each time. The male also fed the female once ~10 m from the nest, after which she left the area, presumably to forage. The female fed the nestling upon her return. The male sang near the nest only once during the timed observation period, but sang more fre-

FIG. 1. ʻAkikiki foraging by excavation on a dead twig of a ʻōlapa tree in the upper Halepaʻakai drainage, Kauaʻi, 22 May 2006. Note the pale color of freshly excavated wood between the birds's feet and the darker color of older, weathered excavations higher on the twig. Photograph by E. A. VanderWerf.

quently earlier in the day when we were occupied with other activities.

The nest tree was one of the larger trees in the area and was prominent in the forest canopy. It had many flowers and was visited often by other birds, including ʻApapane (*Himatione sanguinea*), Japanese White-eyes (*Zosterops japonicus*), and ʻAnianiau (*Hemignathus parvus*). The female ʻAkikiki tolerated the presence of these birds and did not react to them, even when they approached to within ~50 cm of the nest. No ʻAkikiki other than the nesting pair were seen or heard in the vicinity of the nest.

On 27 May 2007, EAV found an ʻAkikiki nest in construction on Mōhihi Ridge. The nesting pair was accompanied by a juvenile, indicating they were attempting to renest. The nest was ~8 m above ground level in a 8.5 m tall ʻōhiʻa tree. The exterior was composed largely of moss and appeared to be complete. One bird, assumed to be the female, brought fine plant fibers to the nest three times from 1410 to 1510 hrs HST and worked on the nest lining. A second bird, assumed to be the male, followed the female closely on two of the visits and called near the nest. The male fed the female once ~20 m from the nest. During the feeding the female fluttered its wings and gave high-pitched twittering calls. The juvenile had pale spectacles typical of immature ʻAkikiki, and had fluffy plumage and foraged clumsily, indicating it hatched earlier in the same season.

DISCUSSION

The nests we observed were similar to other reported ʻAkikiki nests, but the nest found in 2006 was slightly higher above ground level and in a taller tree. Two ʻAkikiki nests reported by Eddinger (1972) were on terminal branches 8.1 and 8.5 m above ground level in the crowns of non-blooming ʻōhiʻa trees, two nests observed during the 2000 Kauaʻi forest bird survey were also in ʻōhiʻa trees, a nest observed in 1999 was 9 m above ground level in a 9.6 m ʻōhiʻa tree (David Kuhn, cited in Foster et al. 2000), two other nests were 4 and 6 m above ground level in ʻōhiʻa (Jim Denny,

FIG. 2. ʻAkikiki nest in the crown of a ʻōhiʻa tree in the upper Halepaʻakai drainage, Kauaʻi, 24 May 2006. The female's head is visible above the nest rim, and downy feathers on the head of a nestling are visible in front of the female. Photograph by E. A. VanderWerf.

cited in Foster et al. 2000), and a nest found in 2005 was 8 or 9 m above ground level in a ʻōhiʻa (Brett Hartl, pers. comm.). The nests reported by Eddinger (1972) were composed primarily of moss. The nest observed in 1999 by David Kuhn had an exterior of moss and a rim and lining of strips of ʻōhiʻa bark, plant rootlets, and other fine plant fibers. At least one of the nests observed by Jim Denny included ʻōlapa bark (Foster et al. 2000). The timing of the nesting attempt we observed in 2006 was within the March-June breeding season described by Foster et al. (2000). The nest observed in 2005 by Brett Hartl was under construction on 29 January, which is earlier than all other known nesting activity. The nest we observed in 2007 would fledge in July, if successful.

There is limited information about the breeding biology of the ʻAkikiki. Nest construction is reported to be by the male and female (Eddinger 1972), and the male is reported to feed the female during nest construction (Foster et al. 2000). Incubation has been observed by the female only, and Eddinger (1972) commented on the tenacity of the female to remain on the nest during incubation despite disturbance. One nest found by Eddinger (1972) contained a single egg and a second nest contained two nestlings. Our observations provide new information. Both male and female ʻAkikiki brought food to the nest, although only the female was observed to broo and feed the nestling. The nestling was fed three times during 1.5 hrs of observation, twice with food provided by the male and once with food provided by the female. The male provided food for the female during brooding, and it is likely that such provisioning occurs throughout the nesting cycle. The female also foraged independently and the relative importance of male provisioning remains unknown. These behaviors are common to other Hawaiian honeycreepers (Lepson and Freed 1997, Lepson and Woodworth 2001, Pratt 2005). The nestling provisioning rate (2.0/hr) and relative contribution of each gender (67% by the male) were similar to those

in the Hawaii Creeper (3.7 provisionings/hr, 57% by the male) (VanderWerf 1998). The pair observed in 2007 was at least attempting to raise two broods in a season, which is unusual among insectivorous Hawaiian honeycreepers. The nesting season is longer than previously reported with activity beginning in January in some years and renesting attempts possibly continuing into July.

'Akikiki are reported to forage on trunks, branches, and twigs of live and dead trees, primarily 'ōhi'a and koa (*Acacia koa*), and occasionally in subcanopy shrubs (Foster et al. 2000). They feed on insects, insect larvae, and other arthropods that are taken by gleaning and probing from bark, crevices, and epiphytes (Foster et al. 2000). There are no previous reports of the excavating behavior that we observed. No other bird on Kaua'i is known to excavate in this manner and it is improbable the 'Akikiki was taking advantage of an excavation begun by another species. The medium-length bill of the 'Akikiki is generally believed to be adapted for gleaning and probing, but our observations indicate it can also be used for excavation. The presence of similar but older and weathered excavation patterns on the same twig suggests it had been excavated previously, perhaps by the same individual 'Akikiki. Excavation may be a more regular foraging behavior in the 'Akikiki than is currently realized.

ACKNOWLEDGMENTS

We thank T. R. Savre and D. L. Leonard for camaraderie in the field, Brett Hartl for information about the nest observed in 2005, D. L. Leonard, C. E. Braun, and two anonymous reviewers for comments that helped improve the manuscript, and the Hawai'i Division of Forestry and Wildlife for continuing support of the Kaua'i Forest Bird Recovery Project.

LITERATURE CITED

Benning, T. L., D. LaPointe, C. T. Atkinson, and P. M. Vitousek. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. Proceedings of the National Academy of Science 99:14246–14249.

Eddinger, C. R. 1972. Discovery of the nest of the Kauai Creeper. Auk 89:673–674.

Foster, J. T., J. M. Scott, and P. W. Sykes Jr. 2000. 'Akikiki (*Oreomystis bairdi*). The birds of North America. Number 552.

Foster, J. T., E. J. Tweed, R. J. Camp, B. L. Woodworth, C. D. Adler, and T. Telfer. 2004. Long-term population changes of native and introduced birds in the Alaka'i Swamp, Kaua'i. Conservation Biology 18:716–725.

International Union for the Conservation of Nature (IUCN). 2006. 2006 IUCN Red list of threatened species. ⟨www.iucnredlist.org⟩ (accessed 17 January 2007).

Lepson, J. K. and L. A. Freed. 1997. 'Ākepa (*Loxops coccineus*). The birds of North America. Number 294.

Lepson, J. K. and B. L. Woodworth. 2001. Hawai'i Creeper (*Oreomystis mana*). The birds of North America. Number 680.

Pratt, H. D. 2005. The Hawaiian honeycreepers. Oxford University Press, Oxford, United Kingdom.

Richardson, F. and J. Bowles. 1964. A survey of the birds of Kauai, Hawaii. B. P. Bishop Museum Bulletin 227.

Scott, J. M., S. Conant, and C. van Riper III. 2001. Evolution, ecology, conservation, and management of Hawaiian birds: a vanishing avifauna. Studies in Avian Biology 22:1–428.

Scott, J. M., S. Mountainspring, F. L. Ramsey, and C. B. Kepler. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Studies in Avian Biology 9:1–431.

U.S. Fish and Wildlife Service (USFWS). 1984. Kauai forest bird recovery plan. USDI, Fish and Wildlife Service, Region 1, Portland, Oregon, USA.

U.S. Fish and Wildlife Service (USFWS). 2004. Review of native species that are candidates or proposed for listing as endangered or threatened; annual notice of findings on resubmitted petitions; annual description of progress on listing actions; notice of review. Federal Register 71:53756–53835.

U.S. Fish and Wildlife Service (USFWS). 2006. Revised recovery plan for Hawaiian forest birds. USDI, Fish and Wildlife Service, Region 1, Portland, Oregon, USA.

VanderWerf, E. A. 1998. Breeding biology and territoriality of the Hawai'i Creeper. Condor 100: 541–545.

The Wilson Journal of Ornithology 120(1):200–201, 2008

First Observation of Duetting in the Olive-backed Euphonia (*Euphonia gouldi*)

Thor Hanson[1]

ABSTRACT.—I observed a pair of Olive-backed Euphonias (*Euphonia gouldi*) in the Caribbean lowlands of Costa Rica singing a prolonged antiphonal duet on 28 February 2006. The male and female were perched near one another within a larger conspecific flock, and exchanged closely-coordinated notes in phrases lasting ~5 sec. This appears to be the first report of duetting behavior for this species or for any member of family Fringillidae. *Received 24 January 2007. Accepted 28 April 2007.*

Duetting behavior in birds has been reported for more than 200 species (Farabaugh 1982) and is the subject of increasing research attention (Langmore 1998, Hall 2004). Functions of duetting remain unclear, but likely include joint territorial defense, mate guarding, and the formation or strengthening of pair bonds (Morton 1996, Langmore 1998, Hall 2004). Duets vary widely in complexity among species (Farabaugh 1982) and may serve different or even multiple purposes in different settings (Marshall-Ball et al. 2006). Duetting is relatively uncommon in northern temperate regions, but occurs more regularly in the tropics where year-round territoriality and long-term pair bonds are common and may encourage its development (Morton 1996, Slater and Mann 2004). Documenting the extent of this behavior in the tropics is far from complete and remains a research priority (Hall 2004). This paper describes the first record of duetting in the Olive-backed Euphonia (*Euphonia gouldi*) and discusses the observation in the context of related literature.

OBSERVATIONS

I observed a pair of Olive-backed Euphonias singing a complex, antiphonal duet on 28 February 2006 in Cantón Sarapíqui, Costa Rica. These observations occurred in the understory of unlogged primary lowland rainforest at the La Selva Biological Station (McDade et al. 1994). I watched a male and female perched ~10 cm from one another on the same branch within a conspecific flock of at least eight individuals. The species is dichromatic and the male and female roles in the duet were identifiable from sex-specific plumage patterns. The female interspersed staccato chips and single-notes seamlessly between the more varied whistled tones of the male. Completed phrases lasted 4–5 sec and were repeated with variations after a brief pause for >2 min. The rest of the flock was dispersed in nearby undergrowth vocalizing with a range of simple whistle tones and calls. No other duets were heard or observed in >10 min of observation.

DISCUSSION

The song of the Olive-backed Euphonia has been described as "a rapid, jerky, rambling melody of rolling *chrrs*, staccato notes, short, clear whistles and more nasal, slurred whistles" (Stiles and Skutch 1989:421). In my observations, the 'staccato notes' and perhaps what Stiles and Skutch describe as 'short, clear whistles' were supplied by the female. The resulting song was continuous and I would have ascribed it to the male alone if both individuals had not been in clear view at close range. Euphonias often frequent the canopy or dense edges and secondary vegetation (Stiles and Skutch 1989), and can be difficult to view clearly. It remains to be learned whether duets are common in this species and what function they might serve. My observations occurred during the beginning of the breeding season (Stiles and Skutch 1989), a time when duets may be involved in regulation of reproductive synchrony (Hall 2004), or the establishment or reaffirmation of pair bonds (Farabaugh 1982).

[1] Department of Forest Resources, University of Idaho, Moscow, ID 83844, USA; e-mail: thor@rockisland.com

I am unaware of reports of duetting from any other member of the subfamily Euphoniinae or the family Fringillidae as currently defined (American Ornithologists' Union 1998). Distinctive and prolonged vocalizations are common in this group, however, and the closely-related Thick-billed Euphonia (*E. laniirostris*) and Violaceous Euphonia (*E. violacea*) are well-documented mimics (Snow 1974, Morton 1976, Remsen 1976). Stiles and Skutch (1989: 420) describe vocalizations for the female Yellow-throated Euphonia (*E. hirundinacea*) as "thin, dry notes, sometimes high-pitched and almost trilled," but they do not report duetting. Future efforts should explore the frequency and purpose of duets in the Olive-backed Euphonia, and observers should be on the alert for duetting behavior in its congeners.

ACKNOWLEDGMENTS

This work was supported in part by NSF-IGERT grant 0114304. The author thanks two anonymous reviewers for helpful comments on the manuscript.

LITERATURE CITED

American Ornithologists' Union. 1998. Checklist of North American birds. Seventh Edition. American Ornithologists' Union, Washington, D.C., USA.

Farabaugh, S. M. 1982. The ecological and social significance of duetting. Pages 85–124 *in* Acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Editors). Academic Press, New York, USA.

Hall, M. L. 2004. A review of hypotheses for the functions of avian duetting. Behavioral Ecology and Sociobiology 55:415–430.

Langmore, N. E. 1998. Functions of duet and solo songs of female birds. Trends in Ecology and Evolution 13:136–140.

Marshall-Ball, L., N. Mann, and J. B. Slater. 2006. Multiple functions to duet singing: hidden conflicts and apparent cooperation. Animal Behavior 71:823–831.

McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Editors). 1994. La Selva: ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, Illinois, USA.

Morton, E. S. 1976. Vocal mimicry in the Thick-billed Euphonia. Wilson Bulletin 88:485–487.

Morton, E. S. 1996. A comparison of vocal behavior among tropical and temperate passerine birds. Pages 258–268 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Editors). Cornell University Press, Ithaca, New York, USA.

Remsen, J. V. 1976. Observations of vocal mimicry in the Thick-Billed Euphonia. Wilson Bulletin 88: 487–488.

Slater, J. B. and N. I. Mann. 2004. Why do the females of many bird species sing in the tropics? Journal of Avian Biology 35:289–294.

Snow, B. K. 1974. Vocal mimicry in the Violaceous Euphonia. Wilson Bulletin 86:179.

Stiles, F. G. and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

The Wilson Journal of Ornithology 120(1):201–204, 2008

The Display of a Reddish Hermit (*Phaethornis ruber*) in a Lowland Rainforest, Bolivia

Adam Felton,[1,2,3] Annika M. Felton,[1,2] and David B. Lindenmayer[1]

ABSTRACT.—The Reddish Hermit (*Phaethornis ruber*) is a commonly encountered hummingbird within the understory of tropical forests from Venezuela to south-east Brazil. Reddish Hermits, like many hummingbirds, perform elaborate displays associated with mate and territory acquisition. We provide the first detailed description with supporting illustrations of intricate displays between two male *P. ruber* to which we refer as "Rotation" and "Arc" displays. *Received 28 December 2006. Accepted 17 July 2007.*

[1] Centre for Resource and Environmental Studies, WK Hancock Building, Australian National University, Canberra, Australia 0200.

[2] Instituto Boliviano de Investigación Forestal (IBIF), Avenue 2 de Agosto esq. Cuarto Anillo Casilla Postal 6204, Santa Cruz de la Sierra, Bolivia.

[3] Corresponding author; e-mail: adamf@cres.anu.edu.au

The Reddish Hermit (*Phaethornis ruber*) is a common inhabitant of tropical forest under-

story from Venezuela to south-east Brazil and is one of the smallest (~2.4 g) known hummingbird species (Oniki 1996). Like many hummingbirds, Reddish Hermits form leks where several males display to females which visit these assemblages to choose a mate (Snow 1973). The displays of Reddish Hermits at leks and in captivity often involve visually spectacular and elaborate aerial maneuvers (Mobbs 1971).

Davis (1934:732) observed the display of a Reddish Hermit in October 1931 and suggested that it "must be seen for its beauty to be appreciated". Over the ensuing decades, several researchers have provided written accounts of Reddish Hermit displays in the wild (Snow 1973) and in captivity (Mobbs 1971). One of these accounts (Snow 1973:171) describes a display performed by a visiting male in front of a territorial male within a lek. The visiting male is described as hovering "8–10 cm above and in front of the owning male" and, as it hovered, "the bird's rear swayed side to side by about an inch while the head remained stationary". Our objective in this paper is to provide the first detailed description, with supporting illustrations, of what appears to be a similar but more extensive display, which we suggest was by a male intruding into the territory of a neighboring male.

OBSERVATIONS

One of us (AF) was conducting bird surveys on 23 August 2004 within the lowland subtropical humid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. This concession is ~300 km north of the lowland city of Santa Cruz. The forest varies in altitude from 230 to 390 m with an average elevation of 320 m. The mean annual temperature is 25° C with mean annual precipitation of ~156 cm. The region experiences a distinct dry season from May to October. One survey point was in a 471-m^2 logging gap (15° 40′ 07 S, 62° 45′ 77 W) created by felling a 60-cm dbh tower tree (*Schizolobium parahyba*; Caesalpiniaceae).

The following observations and sound recording were made in the understory of adjacent pioneer vegetation of two Reddish Hermits at 0620 hrs. The temperature was 14° C with 100% cloud cover and no wind. No conspecifics were noted within the vicinity during these displays, but the observed situation is not inconsistent with the circumstances expected to be found within a lek (Snow 1973).

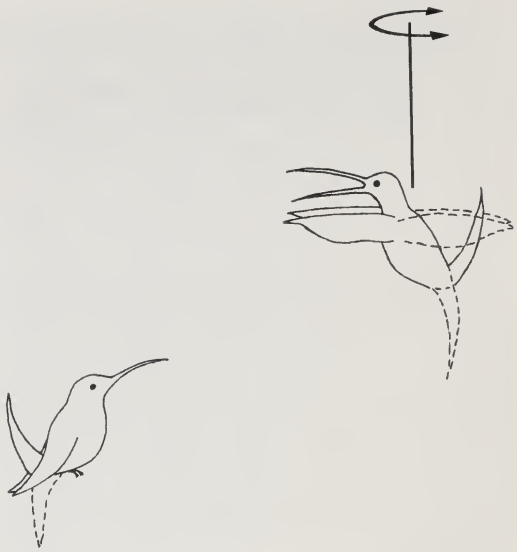


FIG. 1. Illustration of the rotation display of the Reddish Hermit with the perched individual to the left and the displaying individual to the right.

We observed an individual *P. ruber* perched on a branch ~1 m above ground. The perching individual would flick its tail up and down, and occasionally fly to a different perch briefly during the displays of the other individual before returning to the original perch (Fig. 1). The displaying conspecific engaged in an intricate flying display ~25 cm to the front and above the perched individual.

Rotation Display.—We refer to the first display as the "rotation display" (Fig. 1). The displaying individual conspicuously erected white plumage near its flanks, presumably of its thigh feathers. With its back arched and head raised, the bird increased its stroke amplitude to what we perceived was the point of contact (Altshuler and Dudley 2003), due to an accompanying continuous rapid droning sound, which was distinct from that produced during normal flight. We were under the impression that the wings collided at both the ends of the upstroke and the downstroke. The tail was simultaneously raised and lowered with a speed that blurred its image to the human eye. Concurrently the bird yawed through 300° of movement. This was one of the most mesmerizing aspects of the display due to the

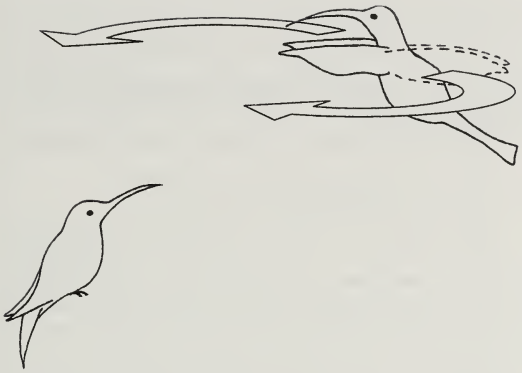


FIG. 2. Illustration of the arc display of the Reddish Hermit with the perched individual to the left and displaying individual to the right.

individual's capacity to avoid any corresponding rolling, pitching, or translational movement. This was done in a punctuated movement (at the start and end point of each arc), taking ~1 sec to complete an arc. At the same time, it rhythmically opened and closed its bill, thereby displaying the vibrant yellow coloration of the gape. All of these movements were characterized by extreme speed and precision and continued in repeated bouts that ranged from 3 to over 75 sec (mean = 15.4 sec; n = 5).

The rotation display was accompanied by a high pitch repetitious song that was made by either the displaying individual or the perched individual. Like Mobbs (1971), we do not feel confident categorically assigning the song to one individual or the other. It consisted of high pitched ascending and descending individual notes and trills (zee'zee'zee'zeezezeze ze'zee), similar to that described by Nicholson (1931) as heard from a *P. ruber* lek in northern Guyana.

Arc Display.—The individual at times switched to alternate, but equally transfixing behavior between rotation displays, which we refer to as the "arc display" (Fig. 2). The displaying individual during this phase remained facing the perched individual and moved laterally over a ~100° arc, as if tethered at the chest to its perching audience. Tail movements may have been related more to controlling flight, than to display. We estimate the amplitude (horizontal distance moved) of this display was ~30 cm. The displaying individual could complete 3 arcs within 1 sec with each arc punctuated by a "diu" call (Fig. 3). This call was consistently between ~1,000 and 2,000 kHz, inconsistent with the frequency of their normal "tsi" call. The arc display was flanked both before and after by the rotation display, and was the shorter of the two displays. The arc display ranged from 1.0 to just over 3.3 sec in length (mean = 2.0 sec, n = 8). The entire display ended suddenly with both individuals moving from the field

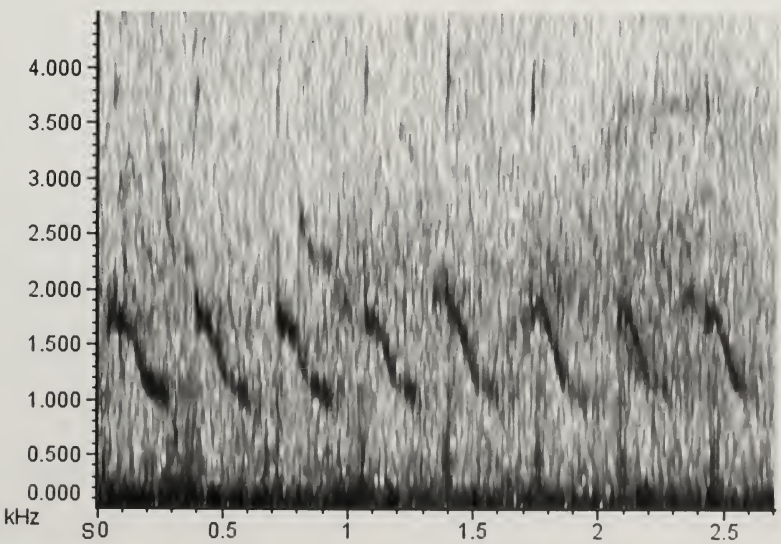


FIG. 3. Spectrogram of "diu" sounds made by Reddish Hermit while performing the arc display.

of view. We are uncertain whether one chased the other away.

DISCUSSION

We have several reasons for suggesting that both individuals were males and this observation was an antagonistic display similar to that described by Snow (1973). Among the hummingbirds, the hermits (Phaethorninae) are notable for their lack of sexually dimorphic characteristics (Höglund 1989). However, it is possible to use plumage characteristics for distinguishing male *P. ruber* from females (Höglund 1989). Both male and female *P. ruber* have a rufous breast, but the male's breast is marked by a black 'V' with the female lacking this mark altogether or possessing an obscure black blemish in its place (Davis 1958, Oniki 1970, Höglund 1989). Both the displaying and the perched individuals in our observations had a black 'V'. We are confident that both individuals were males and the observed behavior was not a courtship display.

Notably, it was the individual with the stronger male coloration that was perched with the displaying individual's black chest bar fainter. This may indicate the displaying individual was a less mature male. This would be concordant with the description by Snow (1973) of a male attempting to displace a more established neighboring territorial owner.

The other indication this display represents antagonistic behavior between two males over what appears to be a lek territory is the season in which the observation occurred. Breeding records for *P. ruber* in this region of Bolivia are absent, but records from Brazil (Oniki 1970), Guyana (Davis 1934, 1958), and Trinidad (Snow 1973) consistently show the breeding season overlaps with the local dry season. The observed display occurred during the middle of the dry season in this region of Bolivia and we are confident this was a breeding-related display.

We believe the most parsimonious explanation for the observed behavior is that it consisted of an encounter between a resident (perching individual) and intruding (displaying) male within what was likely a lek territory. We suggest that more systematic observations are needed before we can gain a thorough understanding of these intricate displays.

ACKNOWLEDGMENTS

This project was supported through the generous financial assistance of the American Ornithologists' Union, Sennheiser Australia, and the Lincoln Park Zoo, Chicago. We thank the personnel of IBIF, Agroindustria Forestal La Chonta Ltd., Proyecto de Manejo Forestal Sostenible (BOLFOR), and Birdlife Bolivia (Armonia) for providing logistical support, especially Marielos Peña and Todd Fredericksen. Eugenio Mercado provided integral assistance during all phases of the field work and the advice of Ross Cunningham greatly contributed to the design of this project. We thank Dan Brooks and an anonymous reviewer for helping us to improve an earlier version of this manuscript. We thank the Australian Red Cross without whom this project could not have been completed. All research was approved by the relevant authorities and this study was conducted within the ethical guidelines of Australia and Bolivia.

LITERATURE CITED

Altshuler, D. L. and R. Dudley. 2003. Kinematics of hovering hummingbird flight along simulated and natural elevational gradients. Journal of Experimental Biology 206:3139–3147.

Davis, T. A. W. 1934. Notes on the display in the humming-birds *Phaethornis superciliosus* (Linn.) and *Pygmonris ruber* (Linn.). Ibis 13:732–738.

Davis, T. A. W. 1958. The displays and nests of three forest hummingbirds in British Guiana. Ibis 100: 31–39.

Höglund, J. 1989. Size and plumage dimorphism in lek-breeding birds: a comparative analysis. American Naturalist 134:72–87.

Mobbs, A. J. 1971. Notes on the Reddish Hermit hummingbird. Aviculturalist Magazine 77:160–163.

Nicholson, E. M. 1931. Communal display in humming-birds. Ibis 13:74–83.

Oniki, Y. 1970. Nesting behavior of Reddish Hermits (*Phaethornis ruber*) and occurrence of wasp cells in nests. Auk 87:720–728.

Oniki, Y. 1996. Band sizes of southeastern Brazilian hummingbirds. Journal of Field Ornithology 67: 397–391.

Snow, B. K. 1973. The behavior and ecology of hermit hummingbirds in the Kanaku Mountains, Guyana. Wilson Bulletin 85:163–177.

The Wilson Journal of Ornithology 120(1):205–209, 2008

Home Range and Habitat Preferences of the Banded Ground-cuckoo (*Neomorphus radiolosus*)

Jordan Karubian[1,3] and Luis Carrasco[2]

ABSTRACT.—The Banded Ground-cuckoo (*Neomorphus radiolosus*) is a rare, endangered, and poorly known species endemic to the Chocó Biogeographic Zone. We summarize 7 months of data from radio tracking an adult in northwestern Ecuador. Home range estimates were 42.2 ha (minimum convex polygon) and 49.9 ha (95% kernel analysis); the core area was 3.4 ha (50% kernel analysis). The bird favored undisturbed habitat and avoided secondary forest. It was primarily insectivorous and rarely associated with army ants (*Eciton* sp.) and not with mammals. Breeding occurred from March through June and the marked bird was seen with an unmarked individual throughout the study. The Banded Ground-cuckoo has a large home range, limited dispersal ability, and apparently depends on undisturbed forest. Deforestation and habitat fragmentation appear to be the gravest threats facing the species. *Received 15 December 2006. Accepted 28 April 2007.*

Ground-cuckoos (*Neomorphus*: Cuculidae) are terrestrial, rain-forest-dwelling birds distributed across the Neotropics (Haffer 1977, Payne 1997). They forage on insects, small vertebrates, and fruit often while associating with army ants (*Eciton* sp.), *Tayassu* peccaries, or *Saimiri*, *Cebus*, and *Saguinas* primates (Sick 1949, Willis and Oniki 1978, Willis 1982, Terborgh 1983, Siegal et al. 1989). Biparental care has been reported for one species (Karubian et al. 2007), and none is thought to be a brood parasite (Sick 1949, Haffer 1977, Roth 1981, Payne 1997). Little else is known about any of the four species of *Neomorphus*, which replace each other geographically.

The Banded Ground-cuckoo (*Neomorphus radiolosus*) is endemic to the Chocó rain forests of northwestern Ecuador and western Colombia. It is one of the rarest birds in either country; in recent years it has been reported from only two localities in Ecuador (Hornbuckle 1997, López-Lanús et al. 1999, Ridgely and Greenfield 2001) and three localities in Colombia (Payne 1997). It is considered "vulnerable to extinction" because of widespread deforestation throughout its range, but a lack of data on habitat requirements, home range, and other basic ecological parameters has hindered assessment of its conservation requirements and status (BirdLife International 2000, Greenfield 2002, Renjifo et al. 2002). We report observations on the home range and habitat use of the Banded Ground-cuckoo based on a 7-month radio-tracking study of an adult in northwestern Ecuador.

METHODS

Our study was conducted at Bilsa Biological Station (79° 45′ W, 0° 22′ N, 330–730 m elevation), a 3,500-ha private reserve within the Mache-Chindul Ecological Reserve in Esmeraldas Province, Ecuador. Bilsa is mostly undisturbed forest but also contains selectively-logged and regenerating forests. The surrounding area is largely deforested but also contains selectively logged and regenerating forests.

We captured an adult Banded Ground-cuckoo in a mist net in December 2002, obtained standard morphological measures, and applied three colored leg bands. We also attached a radio transmitter (model RI-2C, Holohil Systems, Carp, ON, Canada) using a backpack style harness of thin rubber ligature (Vehrencamp and Halpenny 1981). The 6.0-g radio weighed 1.4% of the bird's total body mass of 433 g. Total processing time was 43 min. We tracked the bird over a period of 210 days (until the radio failed) using a Telonics TR4 receiver and a RA-2AK "H" antenna.

We attempted to record a single fix of the bird's location during each radio-tracking session when we first observed the bird or when

[1] Center for Tropical Research, Institute of the Environment, University of California at Los Angeles, La Kretz Hall, Suite 300, Box 951496, Los Angeles, CA 90095, USA.

[2] Javier Zambrano n16-45 y Rió de Janeiro, Quito, Ecuador.

[3] Corresponding author; e-mail: jordank@ucla.edu

we heard a vocalization in combination with a radio signal that indicated the distance between the bird and the researcher was <20 m. We recorded only one fix per day to ensure independence of points. We recorded 53 fixes, 22 (42%) after observing the bird and 31 (58%) after hearing it. We recorded a single fix at each of two nests but suspended radio tracking during nesting to minimize disturbance. We recorded UTM coordinates at each fix using a Garmin GPS and plotted the coordinates using the Animal Movement Analysis extension in ArcView Geographical Information System (Hooge and Eichenlaub 2000). Fixes were visualized as minimum convex polygons (MCP's) (Mohr 1947), and 95% and 50% fixed kernel isopleths using least-squares cross validation (Worton 1989, Seamann and Powell 1996). MCPs are included despite their inherent biases (Powell 2000) to allow comparison with other studies. We recorded the presence or absence of army ants and mammals at radio points and opportunistically recorded social behavior and foraging. We assessed habitat characteristics at 48 fixes using 10-m radius circular plots which were compared to 10-m radius circular control plots of known history (primary forest, selectively-logged forest, and secondary forest regenerating 12–20 years). We estimated canopy height and number of trees in the genera *Cecropia* (Cecropiaceae) and *Miconia* (Melastomataceae) in each circular plot. Both are pioneer tree species that can be used as an index of habitat disturbance. We counted number of trees with a diameter at breast height (dbh) >50 cm in circular plots of 20 m.

We mist netted a second adult on 4 May 2005 near a nest in incubation stage and attached a 6.0-g Holohil RI-2C radio transmitter (1.6% of the bird's body mass of 365 g) with a backpack style harness. Total processing time was 38 min. We used radio tracking and visual observation to confirm this bird resumed normal incubation that same afternoon and continued through 7 May. On 4 June 2005 we discovered the remains of this bird (bones, most of which had been fractured, and feathers scattered over 3 m^2) 420 m from point of capture. We recovered the radio 3 m from the remains. The broken bones and damage to the radio suggest predation by a mammal. We did not obtain any radio points for this bird.

We present data as means ± SE. We analyzed habitat data with pairwise Wilcoxon signed rank tests using $P < 0.05$ as the significance level because the data were not normally distributed. Analyses were conducted using JMP (SAS 2003).

RESULTS

We obtained 53 independent fixes between 5 December 2004 and 7 July 2005. The MCP and kernel analysis home range sizes were, respectively, 42.2 ha and 49.9 ha (Fig. 1). The core use area was 3.4 ha (Fig. 1). Vegetation at fixes differed ($P < 0.05$) from plots in secondary forest in all four parameters considered (Table 1) and from plots in selectively-logged forest in two parameters, but did not differ from primary forest plots in any parameter.

The bird was observed with army ants on five occasions (9.5% of all fixes) but not with mammals. We observed the bird eat seven insects (4 grasshoppers, 3 unknown) that it flushed up and pursued as would a Roadrunner (*Geococcyx* spp.). On one occasion the bird appeared to eat decaying pulp (no larvae were present) of a fallen *Gustavia dodsonii* (Lecythidaceae) seed. Excluding observations at active nests, the radio-equipped bird was seen or heard with another adult Banded Ground-cuckoo on seven occasions (13.2% of fixes) evenly distributed throughout the study period.

Morphological measures for the first and second radio-equipped birds, respectively, were tarsus (73.8 and 77.1 mm), wing chord (150 and 156 mm), tail length (250 and 254 mm), bill depth (19.6 and 16.7 mm), bill width (13.8 and 13.8 mm), culmen from the distal edge of the nare (33.8 and 35.1 mm), and exposed culmen (58.1 and 58.0 mm). The gender of both birds was unclear. The first radio-equipped bird was lightly molting on the body and remiges, and the second bird was heavily molting on the body and remiges, and had an active brood patch.

DISCUSSION

This is the first report of home range size for any Neomorphinae, a sub-family of cuckoos with five New World genera including the Ground-cuckoos and Roadrunners. The Banded Ground-cuckoo's home range of ~50 ha, a

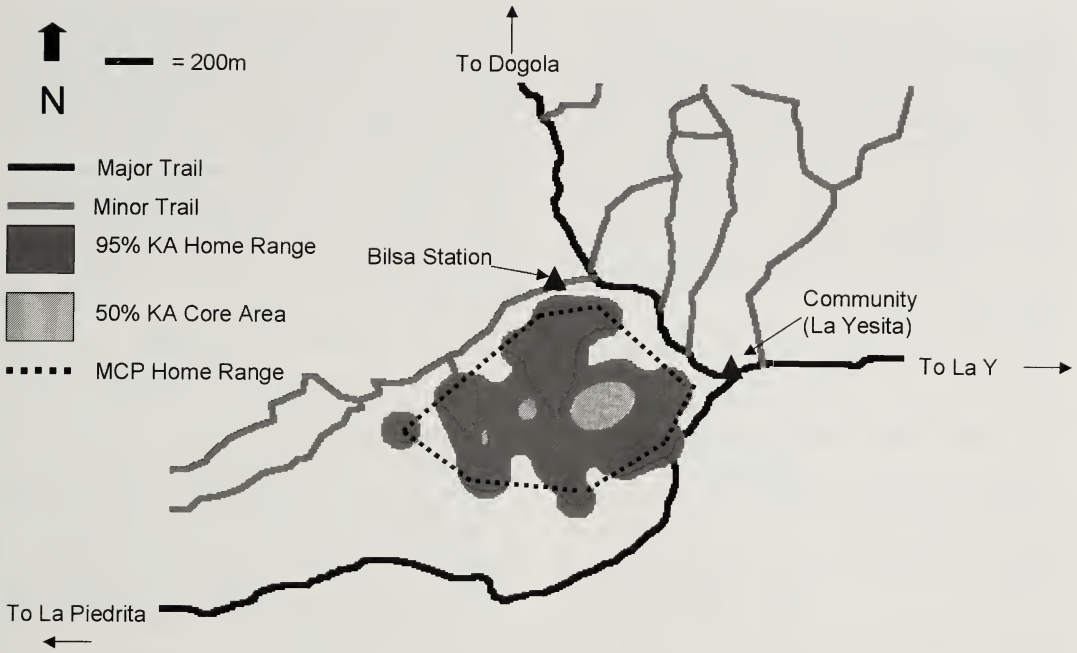


FIG. 1. Minimum convex polygon (MCP) home range and Kernel analysis (KA) home range and core use area of an adult Banded Ground-cuckoo during 7 months in Bilsa Reserve, northwestern Ecuador.

conservative measure because of the study's limited duration, is large relative to other terrestrial rain forest species. Mountain Wood Quail (*Odontophorus hyperythrus*, 275 g) in the Colombian Andes had home ranges of 5.2 ha (Franco et al. 2006) and Chowchilla (*Orthonyx spaldingii*, 150 g) in the Australian Wet Tropics had home ranges of <2 ha (Jansen 1999).

Banded Ground-cuckoos are cryptic, difficult to observe, unlikely to be captured in mist nets, and do not reliably respond to playback, making censuses using traditional methods unreliable. However, local population size can be estimated with home range data. Assuming Bilsa contains 2,000 ha of suitable habitat (e.g., primary forest; Jatun Sacha Foundation, unpubl. data) and the species forms socially monogamous pairs with 50-ha territories, Bilsa could contain ~40 pairs. This emphasizes the reserve's importance for this and other endemics given the widespread deforestation in the Chocó (Sierra 1999, Conservation International 2001).

Army ants are common at Bilsa and the Banded Ground-cuckoo occasionally associated with them (9.5% of fixes) but was not an obligate or even frequent army ant follower as has been previously suggested (Willis and Oniki 1978, Willis 1982, Ridgely and Greenfield 2001). It did not associate with mammals, although this may be due to the rarity of pec-

TABLE 1. Habitat characteristics at Banded Ground-cuckoo radio fix locations versus control plots.

Plot type	Canopy ht. (m)	Trees >50 cm dbh	*Miconia*	*Cecropia*
Radio fixes (n = 48)	23.27 ± 0.94	4.31 ± 0.36	0.64 ± 0.16	0.79 ± 0.26
Control (n = 170)				
Primary (n = 98)	25.26 ± 0.42^{NS}	5.08 ± 0.26^{NS}	0.42 ± 0.15^{NS}	0.48 ± 0.14^{NS}
Selectively-logged (n = 34)	22.38 ± 0.90^{NS}	3.79 ± 0.58^{NS}	1.79 ± 0.42*	2.88 ± 0.68***
Secondary (n = 38)	15.42 ± 1.04***	1.18 ± 0.20***	2.94 ± 0.80**	4.34 ± 0.98***

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ^{NS} = $P > 0.05$.

caries and primates within its home range (JK, unpubl. data). Our observations here in combination with a previous study of the species' nesting biology (Karubian et al. 2007) suggest that large insects and small vertebrates are an important part of the diet. The Banded Ground-cuckoo, as a terrestrial omnivore that primarily captures rapid live prey, fills an unusual ecological niche among neotropical rain forest birds, which may be reflected in its large home range.

The radio-equipped bird was with another adult at least seven times from December into May. The adults maintained vocal but not visual contact when together and often foraged >20 m apart. Breeding extended from March into May and birds exhibited bi-parental care at the nest (Karubian et al. 2007). López-Lanús et al. (1999) recorded an apparent juvenile at Bilsa in February 1997, suggesting the breeding season may begin earlier. The color-banded bird that we radio-tracked in the present study was repeatedly observed in April 2007 close to the 2005 nest sites.

The home range contained a mosaic of habitat types including ~25% secondary forest, but the Banded Ground-cuckoo showed a strong preference for undisturbed forest. Two nesting attempts and care of a newly fledged chick also occurred in primary forest (Karubian et al. 2007). This suggests dependence on primary forest both for nesting and foraging, and corroborates previous assessments of the species' conservation requirements (BirdLife International 2000, Greenfield 2002, Renjifo et al. 2002). Deforestation and fragmentation appear to be the primary threats to the Banded Ground-cuckoo; protection of the remaining primary Chocó rainforest should be high priority for conservation of this species. Other factors contributing to the species' vulnerability may include its relatively large home range, low density, presumably poor dispersal ability, and apparent clutch size of one egg (Karubian et al. 2007).

ACKNOWLEDGMENTS

Jorge Olivo, Domingo Cabrera, Andrew Cook, and Alex Dunn gathered much of the data and J. L. Storey and R. Duřaes assisted with MCP and kernel analyses and maps. We thank each of them for their dedication and excellent work. T. B. Smith provided important intellectual and logistical support. The manuscript was improved by comments from Jügen Haffer and one anonymous reviewer. We also thank the Bilsa Biological Station, especially Carlos Aulestia, Julieta Birmingham, and M. B. McColm. This research was supported by the Chicago Zoological Society; Cleveland Metroparks Zoo; Conservation, Food and Health Foundation; Disney Wildlife Conservation Fund; National Geographic Society; and National Science Foundation (OISE-0402137). All research was conducted with permission from Fundación Jatun Sacha and with approval of the Ecuadorian Ministry of the Environment (Permit 009-CI-FAU-DRE-MA), and the University of California, Los Angeles.

LITERATURE CITED

BirdLife International. 2000. Threatened birds of the world. BirdLife International and Lynx Ediciones, Barcelona, Spain.

Conservation International. 2001. Ecosystem profile: Chocó-Manabi conservation corridor of Chocó-Darien-western Ecuador hotspot. Conservation International, Washington, D.C., USA.

Franco, P., K. Fierro-Calderon, and G. Kattan. 2006. Population densities and home range sizes of the Chestnut Wood-quail. Journal of Field Ornithology 77:85–90.

Greenfield, P. 2002. *Neomorphus radiolosus*. *in* Libro rojo de las aves del Ecuador (T. Granizo, C. Pacheco, M. B. Ribadeneira, M. Guerrero, and L. Suarez, Editors). Simbioe, Conservation International, EcoCiencia, Ecuadorian Ministerio del Ambiente and IUCN, Quito.

Haffer, J. 1977. A systematic review of the neo-tropical Ground-cuckoos (Aves, *Neomorphus*). Bonner Zoologische Beitraege 28:48–76.

Hooge, P. N. and B. Eichenlaub. 2000. Animal movement extension for Arcview Version 2.04. USGS, Alaska Science Center, Biological Sciences Office, Anchorage, USA.

Hornbuckle, J. 1997. Two sightings of Banded Ground-cuckoo *Neomorphus radiolosus* in Ecuador. Cotinga 8:90.

Jansen, A. 1999. Home ranges and group-territoriality in Chowchillas *Orthonyx spaldingii*. Emu 99:280–290.

Karubian, J., L. Carrasco, D. Cabrera, A. Cook, and J. Olivo. 2007. Nesting biology of the Banded Ground-cuckoo (*Neomorphus radiolosus*). Wilson Journal of Ornithology 119:221–227.

López-Lanús, B., K. Berg, R. Strewe, and P. G. W. Salaman. 1999. The ecology and vocalisations of Banded Ground-cuckoo *Neomorphus radiolosus*. Cotinga 11:42–45.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.

Payne, R. B. 1997. Family Cuculidae (cuckoos). *In* Handbook of the birds of the world. Volume 4. Sandgrouse to cuckoos (J. del Hoyo, A. Elliott, and J. Sargatal, Editors). Lynx Ediciones, Barcelona, Spain.

Powell, R. A. 2000. Research techniques in animal

ecology: controversies and consequences. Columbia University Press, New York, USA.

Renjifo, L. M., A. M. Franco-Maya, J. D. Amaya-Espinel, G. H. Kattan, and B. López-Lanús. 2002. Libro rojo de aves de Colombia. Instituto de investigación de Recursos Biológicos Alexandex von Humboldt y Ministerio del Medio Ambiente, Bogotá, Colombia.

Ridgely, R. S. and P. Greenfield. 2001. The birds of Ecuador. Cornell University Press, Ithaca, New York, USA.

Roth, P. 1981. A nest of the Rufous-vented Ground-cuckoo (*Neomorphus geoffroyi*). Condor 83:388.

SAS. 2003. JMP statistical software. SAS Institute Inc., Cary, North Carolina, USA.

Seamann, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Sick, H. 1949. Beobachtungen an dem brasilianischen bodenkuckkuck *Neomorphus geoffroyi dulcis* Snethlage. Pages 229–239 *in* Ornithologie als biologische Wissenschaft. Stresemann-Festschrift, Heidelberg, Germany.

Siegal, C. E., J. M. Hamilton, and N. R. Castro. 1989. Observations of the Red-billed Cuckoo (*Neomorphus pucheranii*) in association with tamarins (*Saguinas*) in northeastern Amazonian Peru. Condor 91:720–722.

Sierra, R. 1999. Vegetación remanente del Ecuador Continental. Circa 1996. 1:1,000,000. Proyecto INEFAN/GEF y Wildlife Conservation Society, Quito, Ecuador.

Terborgh, J. 1983. Five New World primates: a study in comparative ecology. Princeton University Press, Princeton, New Jersey, USA.

Vehrencamp, S. L. and L. Halpenny. 1981. Capture and radio-transmitter attachment techniques for Roadrunners. North American Bird Bander 6: 128–132.

Willis, E. O. 1982. Ground-cuckoos (Aves: Cuculidae) as army ant followers. Revista Brasileira de Biologia 42:753–756.

Willis, E. O. and Y. Oniki. 1978. Birds and army ants. Annual Review of Ecology and Systematics 9: 243–246.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution of home range studies. Ecology 70:164–168.

The Wilson Journal of Ornithology 120(1):209–213, 2008

Comparisons between Juvenile and Adult American Robins Foraging for Mulberry Fruit

E. Natasha Vanderhoff[1,2,3] and Perri K. Eason[1]

ABSTRACT.—American Robins (*Turdus migratorius*) depend on fruit in fall and winter and, accordingly, juvenile robins must quickly learn to acquire this resource. We compared the foraging abilities of juveniles and adults foraging for mulberries (*Morus* spp.), the first fruit that ripens after juveniles have become independent. Juveniles were significantly less successful than adults at obtaining mulberries; 23% of juveniles' attempts to remove fruit were successful compared to 69% of attempts by adults to remove fruit. As a result, juveniles consumed 0.4 mulberries/min whereas adults consumed 2.8 mulberries/min. Further investigations of juveniles' ability to forage for fruit are needed to understand the mechanisms involved in the development of skills to forage for this vital resource. *Received 20 February 2007. Accepted 17 June 2007.*

Foraging for fruit is often assumed to be an easily acquired skill, unlike foraging for animal prey (Stevens 1985, Desrochers 1992, Ricklefs 2004). Support for this assumption regarding avian fruit foraging, however, is mixed. Analyses of stomach contents at times show that juveniles consume more fruit than adults, which suggests that fruits are relatively easily obtained (Wheelwright 1986, Eggers 2000). In addition, some studies found no differences in foraging behavior or rates of fruit consumption between juveniles and adults (European Robin [*Erithacus rubecula*], Common Blackbird [*Turdus merula*], Eurasian

[1] Department of Biology, University of Louisville, Louisville, KY 40292, USA.

[2] Current address: Department of Biology, Francis Marion University, Florence, SC 29501, USA.

[3] Corresponding author; e-mail: evanderhoff@fmarion.edu

Blackcap [*Sylvia atricapilla*]; Hampe 2001, Bas et al. 2006). However, juveniles often consume different types of fruits than adults, which could be a result of differences in foraging abilities (Boddy 1991), and tests of skill level and acquisition of skill have yet to be thoroughly conducted.

If juveniles are less skilled at foraging for fruit, their lower proficiency could be costly, especially for individuals of the many species that depend on fruit for migration and overwintering (Willson 1986, Blake and Loiselle 1992, Levey and del Rio 2001, McCarty et al. 2002, Heise and Moore 2003, Kwit et al. 2004). Juvenile birds often have lower survival rates than adults and starvation is a major cause of juvenile mortality (Sullivan 1988, Catterall et al. 1989, Donnelly and Sullivan 1998). Accordingly, juveniles of migratory species and those that have high mortality should be expected to develop their fruit-foraging skills quickly.

One species that relies heavily on fruit for migration and overwintering is the American Robin (*Turdus migratorius*). The diet of the robin is composed primarily of fruit from late summer through winter (Wheelwright 1986). We compared foraging rates on mulberry fruit (*Morus* spp.) to investigate whether juveniles were less successful at foraging on fruit than adults. Mulberry is the first tree to fruit after juveniles begin to forage independently at our study site in Louisville, Kentucky. Accordingly, we were able to compare naïve juveniles to experienced adults in their ability to forage on this fruit. Our specific objectives were to: (1) quantify and note differences in the outcome of mulberry foraging bouts by juveniles and adults and (2) examine whether or not juveniles and adults differ in their rates of successful and failed attempts to pick mulberries.

METHODS

We investigated juvenile and adult robins' ability to forage for mulberry fruit from 25 May until 23 June 2006 at Joe Creason Park in Louisville, Kentucky (38° 12′ N, 85° 42′ W). Both adult and juvenile robins foraged in fruiting trees simultaneously at our field site and there was little apparent competition between age groups. We conducted continuous focal scans on 64 American Robins (38 adult scans and 26 juvenile scans) foraging for mulberries on trees scattered throughout the 27.5-ha park. Robins typically flew into the trees, ate fruit, and left relatively quickly; therefore, each scan started when a focal bird entered a mulberry tree and ended when it left the tree or was no longer visible. Samples ranged in length from 10 to 243 sec with the average scan lasting a little over a minute (mean ± SE = 67 ± 5.5 sec).

We recorded four behaviors to assess the ability of juveniles and adults to forage for mulberries. First, when a robin unsuccessfully tried to pick a mulberry, we categorized it as a failure. Typically, a failure resulted when a robin was either unable to reach a fruit or unable to pull sufficiently hard to detach the mulberry. Second, when a robin successfully picked and ate a whole mulberry we recorded it as an 'eat'. Third, because each mulberry is composed of multiple drupelets, robins at times picked and ate only a part of one mulberry; we recorded this as 'piece'. Finally, if a robin picked a fruit, but subsequently dropped it, we called it a 'drop'.

We calculated percent success (number of eats/total attempted picks) and percent failure (number of fails/total attempted picks) for each adult and juvenile scan, and compared adult and juvenile scans using a MANOVA followed by individual ANOVAs. We also calculated fruit capture rate (number of eats/min) and fruit failure rate (number of failures/min) for all scans, and compared juvenile scans and adult scans using a MANOVA and follow-up ANOVAs. Fruit failure rate was transformed to meet MANOVA assumptions as follows: transformed fruit failure rate = 1/(1 + failure rate). Few robins dropped fruit and robins seldom picked only a piece of the mulberry. The piece and drop data did not meet MANOVA assumptions, and could not be successfully transformed. We excluded these data from the MANOVA analyses and instead used two Fisher's exact tests to examine whether a greater proportion of juveniles engaged in these behaviors than adults. Means ± SE are reported from non-transformed data and SAS© (2003) was used for all statistics.

RESULTS

Juvenile American Robins were significantly less skilled at obtaining mulberries than

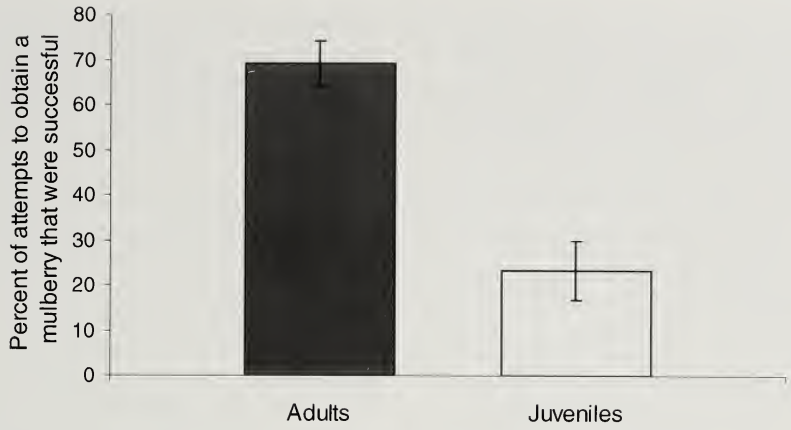


FIG. 1. Juvenile vs. adult American Robins' success at obtaining mulberries.

adults (MANOVA: Wilks' Lambda $F_{2,59}$ = 15.27, $P < 0.001$); only 23 ± 6.4% of attempts to pick mulberries by juveniles were successful compared to 69 ± 5.2% for adults (ANOVA: $F_{1,60}$ = 29.55, $P < 0.001$; Fig. 1). In addition, a significantly larger percentage of attempts by juveniles ended in failure (ANOVA: $F_{1,60}$ = 25.41, $P < 0.001$; juvenile mean = 64 ± 6.7%, adult mean = 23 ± 4.6%). Foraging rates were also significantly different between juveniles and adults (MANOVA: Wilks' Lambda $F_{2,61}$ = 24.74, $P < 0.001$). Juveniles consumed significantly fewer mulberries per minute than adults (ANOVA: $F_{1,62}$ = 49.96, $P < 0.001$) with juveniles consuming less than one mulberry/min (0.4 ± 0.14) and adults consuming nearly three mulberries/min (2.8 ± 0.26; Fig. 2). Juveniles also had a higher rate of failure than adults (ANOVA: $F_{1,62}$ = 4.11, $P < 0.047$) with juveniles, on average, having 1.65 (±0.33) failures/min and adults having 1.04 (±0.22) failures/min. Both juveniles and adults seldom dropped a mulberry once it was picked; only 4% of juveniles and 5% of adults had drops (Fisher's exact test, P = 1.00). There was no significant difference in the proportion of adults and juveniles which consumed only a piece of a mulberry (Fisher's exact test, P = 0.52).

DISCUSSION

Juvenile American Robins were less proficient mulberry foragers than adults; they were less successful at obtaining mulberry fruit and consumed significantly fewer mulberries per minute than adults. Our results strongly indicate that juvenile robins need to develop skills to forage for fruit.

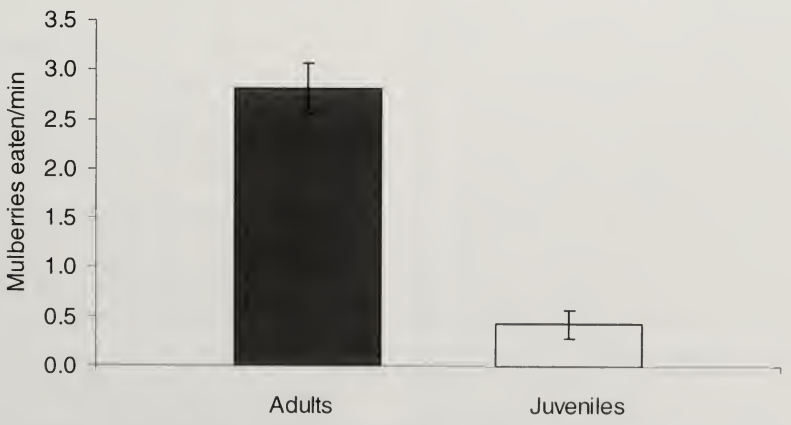


FIG. 2. Juvenile vs. adult American Robins' fruit capture rate per minute.

Other studies have found no differences in foraging rates between juveniles and adults foraging for fruit (Hampe 2001, Bas et al. 2006). One reason for the disparity may be that other researchers observed juveniles that had already developed their skills to forage for fruit. Mulberry, in our study, was the first fruit that juvenile robins learned how to obtain, and the disparity between juveniles and adults may be greatest at this time. If experience is a critical factor in development of foraging skills, juveniles should show improvement when foraging on other fruits later in the season. There is some supporting evidence for this at our field site, where juvenile robins had higher success at obtaining and consuming cherries, which fruit later in the season (Vanderhoff and Eason 2007).

Fruit type may also be an important factor in why some studies found no differences between juveniles and adults. First, fruit type can influence foraging rates; a previous investigation of robins foraging for fruit found that fruit type and, more specifically, size and clustering of fruits within a plant were important in affecting rates of fruit consumption for adults (White and Stiles 1991). Second, type of fruit may also influence the level of skill required to obtain it. Whereas some fruits may be more challenging to acquire and require experience, other fruits may require little or no experience to obtain. For example less experienced Common Whitethroats (*Sylvia communis*) foraged primarily for woody nightshade (*Solanum dulcamara*) berries, a simple fruit, while older birds were able to forage for aggregate blackberries (*Rubus fruticosus*) (Boddy 1991). Similarly, in our study less experienced juveniles had difficulty obtaining mulberry fruit which, like blackberry, is not a simple fruit. Studies that have not found differences between juveniles and adults have focused on simple fruits that may require little or no experience to obtain (glossy buckthorn [*Frangula alnus*], Hampe 2001; Italian buckthorn [*Rhamnus alaternus*], Bas et al. 2006).

Juveniles may be less adept at obtaining fruit than adults due to either physical or cognitive constraints. Gape size is a limiting factor in fruit selection (Wheelwright 1985, Snow and Snow 1988) and juveniles in some species may not have a sufficient gape to obtain certain fruits. However, previous investigations have shown that juvenile gape size does not seem to limit fruit choice or ingestion (White and Stiles 1991, Jung 1992). Cognitive abilities of juveniles may not be fully developed leading to less proficient fruit foraging. For instance, juveniles are often less adept at identifying suitable food items (Whitehead 1984, Caro 1994, Estes et al. 2003). This suggests that juvenile robins may be less able to recognize ripe fruits and, thus, may attempt to pick a higher percentage of unripe fruits. Fruit ripeness can have a two-fold effect on foraging rates; it can result in higher failure rates because fruits cannot be removed or lower consumption rates due to the increased amount of time to remove unripe fruit.

Fruit is a vital resource for birds and it is surprising that relatively few studies have investigated foraging for fruit by juveniles, and the mechanisms involved in their foraging decisions. Our results show that juvenile robins are less proficient at foraging for fruits than adults casting doubt on the assumption that foraging for fruit requires little or no skill acquisition. The assumption that foraging for fruit is easier than other tasks may be accurate; we did not examine this aspect of the development of skills of robins. Future research should be conducted to understand how the rate at which juveniles develop skills at foraging for fruit compares to the rate at which they learn to forage for other food items, as well as the mechanisms that underlie the learning process. Answering these questions will lead to a better understanding of the factors that affect foraging for fruit and add to our knowledge of animal learning, and plant-animal interactions.

ACKNOWLEDGMENTS

We thank C. J. Byers, C. J. Hanna, L. B. Rifai, and T. C. Pelletier for helpful comments on the manuscript. We also thank Louisville Metro Parks for permission to conduct the study at Joe Creason Park.

LITERATURE CITED

Bas, J. M., P. Pons, and C. Gómez. 2006. Exclusive frugivory and seed dispersal of *Rhamnus alternus* in the bird breeding season. Plant Ecology 183: 77–89.

Blake, J. G. and B. A. Loiselle. 1992. Fruits in the diets of neotropical migrant birds in Costa Rica. Biotropica 24:200–210.

Boddy, M. 1991. Some aspects of frugivory by bird

populations using coastal dune scrub in Lincolnshire. Bird Study 38:188–199.

Caro, T. M. 1994. Hunting and grouping in adolescence. Pages 161–197 *in* Cheetahs of the Serengeti. University of Chicago Press, Chicago, Illinois, USA.

Catterall, C. P., J. Kikkawa, and C. Gray. 1989. Inter-related age-dependent patterns of ecology and behaviour in a population of Silvereyes (Aves: Zosteropidae). Journal of Animal Ecology 58:557–570.

Desrochers, A. 1992. Age and foraging success in European Blackbirds: variation between and within individuals. Animal Behaviour 43:885–894.

Donnelly, R. E. and K. A. Sullivan. 1998. Foraging proficiency and body condition of juvenile American Dippers. Condor 100:385–388.

Eggers, S. 2000. Compensatory frugivory in migratory *Sylvia* warblers: geographical responses to season length. Journal of Avian Biology 31:63–74.

Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. Individual variation in prey selection by sea otters: patterns, causes, and implications. Journal of Animal Ecology 72:144–155.

Hampe, A. 2001. The role of fruit diet within a temperate breeding bird community in southern Spain. Bird Study 48:116–123.

Heise, C. D. and F. R. Moore. 2003. Age-related differences in foraging efficiency, molt, and fat deposition of Gray Catbirds prior to autumn migration. Condor 105:496–504.

Jung, R. E. 1992. Individual variation in fruit choice by American Robins (*Turdus migratorius*). Auk 109:98–111.

Kwit, C., D. J. Levey, C. H. Greenberg, S. F. Pearson, J. P. McCarty, S. Sargent, and R. L. Mumme. 2004. Fruit abundance and local distribution of wintering Hermit Thrushes (*Catharus guttatus*) and Yellow-rumped Warblers (*Dendroica coronata*) in South Carolina. Auk 121:46–57.

Levey, D. J. and C. M. del Rio. 2001. It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. Auk 118:819–831.

McCarty, J. P., D. J. Levey, C. H. Greenberg, and S. Sargent. 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. Forest Ecology and Management 164:277–291.

Ricklefs, R. E. 2004. The cognitive face of avian life histories. Wilson Bulletin 116:119–133.

SAS. 2003. SAS system. Version 9.1 for Windows. SAS Institute, Cary, North Carolina, USA.

Snow, B. and D. Snow. 1988. Birds and berries. T. & A. D. Poyser Limited, Carlton, United Kingdom.

Stevens, J. 1985. Foraging success of adult and juvenile Starlings *Sturnus vulgaris*: a tentative explanation for the preference of juveniles for cherries. Ibis 127:341–347.

Sullivan, K. A. 1988. Ontogeny of time budgets in Yellow-eyed Juncos: adaptation to ecological constraints. Ecology 69:118–124.

Vanderhoff, E. N. and P. K. Eason. 2007. Disparity between adult and juvenile American Robins *Turdus migratorius* foraging for ground invertebrates and cherry fruits. Ethology 113:1212–1218.

Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66:808–818.

Wheelwright, N. T. 1986. The diet of American Robins: an analysis of U.S. Biological Survey records. Auk 103:710–725.

White, D. W. and E. W. Stiles. 1991. Fruit harvesting by American Robins: influence of fruit size. Wilson Bulletin 103:690–692.

Whitehead, J. M. 1984. Development of feeding selectivity in mantled howling monkeys, *Alouatta palliate*. Pages 105–117 *in* Primate ontogeny, cognition, and social behavior (J. G. Else and P. C. Lee, Editors). Cambridge University Press, Cambridge, United Kingdom.

Willson, M. F. 1986. Avian frugivory and seed dispersal in eastern North America. Current Ornithology 3:223–279.

The Wilson Journal of Ornithology 120(1):214–216, 2008

Previously Unknown Food Items in the Diet of Six Neotropical Bird Species

Luis Sandoval,[1,3] Esteban Biamonte,[1] and Alejandro Solano-Ugalde[2]

ABSTRACT.—We report new food items for six species of Costa Rican birds. This report includes the first egg predation observed for Hoffman's Woodpecker (*Melanerpes hoffmannii*), the first vertebrate recorded in the diet of Sooty Thrush (*Turdus nigrescens*), and records for Groove-billed Ani (*Crotophaga sulcirostris*), Black-and-white Owl (*Strix nigrolineata*), Blue-crowned Motmot (*Momotus momota*), and Clay-colored Thrush (*Turdus grayi*). *Received 24 January 2007. Accepted 3 May 2007.*

Basic knowledge of the diet of bird species is fundamental to understanding their ecological requirements and designing effective conservation plans for their protection (Kantak 1979, Barrantes and Loiselle 2002). Unfortunately, our understanding of the diets of wild tropical birds is poor. New food items are continuously being added (Chacón-Madrigal and Barrantes 2004, Garcia-C. and Zahawi 2006) to the known diets for even well-studied species, such as motmots (Skutch 1945, 1947, 1964, 1971; Orejuela 1980; Remsen et al. 1993). The results of these studies indicate that many species have a more varied diet than was previously thought.

Information on the diets of Costa Rican birds was generally and briefly summarized by Stiles and Skutch (1989). We report here additional diet items for five species which have a wide distribution in the Neotropics (Stiles and Skutch 1989, Stotz et al. 1996) and present more information about their diets than has been available (Ibañez et al. 1992, Gerhardt et al. 1994, Eitniear and Aragon-Tapia 2000). One of these species, the Sooty Thrush (*Turdus nigrescens*), is endemic in the highlands of Costa Rica and Panamá (Stiles and Skutch 1989, Stotz et al. 1996), and has not had detailed study of its diet. Our specific objective is to provide information on undocumented food items eaten by six species of Costa Rican birds that we recorded over the last 5 years during fieldwork throughout the country.

SPECIES ACCOUNTS

Groove-billed Ani (*Crotophaga sulcirostris*). We observed an ani holding a Ground-sparrow (*Melozone* sp.) egg in its bill on 6 July 2005 at Getsemani, Heredia (10° 06′ N, 84° 02′ W; 1,350 m). The eggshell was whitish with small reddish spots characteristic of the genus (Stiles and Skutch 1989). We earlier (1 week) saw a White-eared Ground Sparrow (*M. leucotis*) with nest material in its bill, 50 m from where the ani was first found and it is possible the egg belonged to this species. The ani swallowed the egg contents through a hole in the eggshell. This is the second record of egg predation by the Groove-billed Ani (Eitniear and Aragon-Tapia 2000) and the first for the tropics. The Smooth-billed Ani (*C. ani*) (Alvarez 1975) and the Groove-billed Ani are the only species in the genus that have been observed eating eggs.

Black-and-white Owl (*Strix nigrolineata*). We observed a Black-and-white Owl on 6 April 2005 at Altamira Station, La Amistad International Park (9° 01′ N, 83° 00′ W; 1,382 m) fly to a cecropia tree (*Cecropia* sp.) at 1745 hrs with a Barn Swallow (*Hirundo rustica*) in its claws where another Black-and-white Owl was perched. The first owl passed the swallow from its bill to the bill of the second owl in ~2 sec. The second owl ate the swallow in one gulp after biting the neck and head while the swallow was held in its claw. Birds are known to be part of the diet of the Black-and-white Owl (Ibañez et al. 1992, Gerhardt et al. 1994), but predation on Barn Swallows has been not previously reported. Barn

[1] Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca, Costa Rica.

[2] Casa #6, Coopecabañas, Santa Ana, San José, Costa Rica.

[3] Corresponding author; e-mail: biosandoval@hotmail.com

Swallows roost on cables in open areas during migration (Skutch 1944); this behavior can make it easy prey for nocturnal predators (McIlhenny 1937, LaPorte 1974). Predation of swallows by other species of related neotropical owls has not been reported, although owl predation on birds is not rare (Marks et al. 1999).

Blue-crowned Motmot (*Momotus momota*). We found an individual Blue-crowned Motmot on 24 September 2003 eating a shrew (*Cryptotis* sp.) (estimated length of 6 cm) at Coronado, San José (9° 57′ N, 83° 59′ W; 1,500 m). The motmot was first seen on the ground in a house garden with the prey in its bill. The motmot repeatedly hit the shrew against the ground for about 5 min and then flew to a higher perch where it swallowed the prey after repeated smashing it for ~2 min. We could see the silhouette of the shrew in the bird's crop after swallowing; the motmot remained motionless for at least 5 min before departing. Several authors report this species of motmot commonly feeds on small vertebrates such as birds, toads, lizards, and snakes (Skutch 1983, Stiles and Skutch 1989, Ridgely and Gwynne 1989), but small mammals are taken rarely (Chacón-Madrigal and Barrantes 2004). We suspect the shrew may have been at the upper size limit of prey consumed by this species based on the manner in which the motmot manipulated it.

We observed a Blue-crowned Motmot on 4 March 2004 on the Universidad de Costa Rica Campus, in San José (9° 54′ N, 84° 03′ W; 1,200 m), eating a portion of wasp nest of about 5 cm in length. The bird struck the wasp nest fragment against the ground in a manner similar to that used for subduing animal prey. It was not possible to identify the content of the nest fragment. The Blue-crowned Motmot is known to consume social insects, such as ants and wasps, as part of its diet (Skutch 1983, Raw 1997, Ridgely and Greenfield 2001), but attacks on wasp nests were previously unknown.

Hoffmann's Woodpecker (*Melanerpes hoffmannii*). We observed an individual Hoffmann's Woodpecker on 9 March 2004 at Coronado, San José (9° 58′ N, 83° 59′ W; 1,500 m) eating an unidentified bird egg, which was completely white and no longer than 2 cm. The woodpecker flew into a single tree in a semi-open area holding the egg in its bill. After arriving at a perch, the bird climbed the tree to a fork where it placed the egg and began to peck a hole into the egg. The bird then started feeding on the contents by rapidly sticking its tongue in and out of the hole in the egg. Woodpeckers have a worldwide distribution and have previously been observed consuming eggs in four species of *Melanerpes*, two species of *Picus*, the Red-naped Sapsucker (*Sphyrapicus nuchalis*), Great Spotted Woodpecker (*Dendrocopos major*), and Cuban Green Woodpecker (*Xiphidiopicus percussus*) (Bryant 1921, Fajer et al. 1987, Cooper 1992, Winkler and Christie 2002).

Sooty Thrush (*Turdus nigrescens*). We saw a Sooty Thrush eating a lizard (*Mesaspis monticola*) on 28 May 2001 at Chirripó National Park (9° 27′ N, 83° 26′ W; 3,600 m). When first observed, the bird was on the ground and had the lizard in its bill, constantly hitting it against the rocky ground surface. The action of hitting the prey on the ground appeared challenging as the thrush took five rests during 3 min of observation. The bird placed the lizard on the ground for periods of about 15 sec throughout the resting periods. The thrush then walked into the dense vegetation with the lizard and disappeared where it is presumed the prey was consumed. The Sooty Thrush inhabits an area in which the lizard *Mesaspis monticola* is abundant (Savage 2002), but has not been previously reported feeding on this lizard. Previous observations indicate that berries and small invertebrates constitute the bulk of the diet of the Sooty Thrush (Stiles and Skutch 1989, Clement 2000).

Clay-colored Thrush (*Turdus grayi*). We observed a Clay-colored Thrush feeding on a house gecko (*Hemidactilus frenatus*) on 31 January 2005 at Golfito, Puntarenas (08° 39′ N, 83° 09′ W; 5 m) while perched on the lawn in front of the Universidad de Costa Rica student houses. The Clay-colored Thrush squashed the gecko's head by repeatedly closing and opening its bill for approximately 40 sec. The bird then moved its head back and with small lateral movements swallowed the gecko. This thrush is mainly frugivorous, but lizards and snakes have been documented as constituting a part of its diet (Feduccia 1971, Stiles and Skutch 1989, Clement 2000); however this gecko species has not previously

been reported in the diet of the Clay-colored Thrush. The house gecko, despite being a recent colonist (Savage 2002), was recently reported as part of the diet of the House Wren (*Troglodytes aedon*) (Barquero and Hilje 2005), indicating this invasive species has become a new food resource for some species.

ACKNOWLEDGMENTS

We thank Julio Sánchez, Joseph Wunderle, C. E. Braun, and an anonymous reviewer for valuable comments on an earlier draft of the manuscript. We also thank Alisson Olivieri, L. D. Holtzman, and C. E. Braun for suggestions that improved our English redaction. We offer our most sincere thanks to all the persons who supported and encouraged our fieldwork throughout the past years.

LITERATURE CITED

Alvarez, H. 1975. The social system of the Green Jay in Colombia. Living Bird 14:5–44.

Barquero, M. and B. Hilje. 2005. House Wren preys on introduced gecko in Costa Rica. Wilson Bulletin 117:204–205.

Barrantes, G. and B. Loiselle. 2002. Reproduction, habitat use, and natural history of the Black-and-Yellow Silky-flycatcher (*Phainoptila melanoxantha*), an endemic bird of the western Panama-Costa Rica highlands. Ornitología Neotropical 13: 121–136.

Bryant, H. 1921. California Woodpecker steals eggs of Wood Pewee. Condor 23:33.

Chacón-Madrigal, E. and G. Barrantes. 2004. Blue-crowned Motmot (*Momotus momota*) predation on a long-tongued bat (Glossophaginae). Wilson Bulletin 116:108–110.

Clement, P. 2000. Thrushes. Princeton University Press, Princeton, New Jersey, USA.

Cooper, J. 1992. Egg eating by a Red-naped Sapsucker (*Sphyrapicus nuchalis*). Northwestern Naturalist 73:59–60.

Eitniear, J. and A. Aragon-Tapia. 2000. Red-billed Pigeon (*Columba flavirostris*) nest predated by Groove-billed Ani (*Crotophaga sulcirostris*). Ornitología Neotropical 11:231–232.

Fajer, E., K. Schmidt, and J. Eschler. 1987. Acorn Woodpecker predation on Cliff Swallow nests. Condor 89:177–178.

Feduccia, A. 1971. *Turdus grayi* feeding on a snake. Auk 83:197.

Garcia-C., J. M. and R. A. Zahawi. 2006. Predation by a Blue-crowned Motmot (*Momotus momota*) on a hummingbird. Wilson Journal of Ornithology 118:261–263.

Gerhardt, R., D. McAnnis-Gerhardt, C. Flatten, and N. Bonilla-Gonzales. 1994. The food habits of sympatric *Ciccaba* owls in northern Guatemala. Journal of Field Ornithology 65:258–264.

Ibañez, C., C. Ramo, and B. Busto. 1992. Notes on food habits of the Black and White Owl. Condor 94:529–531.

Kantak, G. 1979. Observation on some fruits-eating birds in Mexico. Auk 96:183–186.

La Porte, P. 1974. Common Grackle kills a Barn Swallow. Wilson Bulletin 86:477–478.

Marks, J. S., R. J. Canning, and H. Mikkola. 1999. Family Strigidae (typical owls). Pages 76–242 *in* Handbook of the birds of the world. Volume 5. Barn-owls to hummingbirds (J. del Hoyo, A. Elliot, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

McIlhenny, E. A. 1937. Life history of the Boat-tailed Grackle in Louisiana. Auk 54:274–295.

Orejuela, J. 1980. Niche relationships between Turquoise-browed and Blue-crowned motmots in the Yucatan Peninsula, Mexico. Wilson Bulletin 92: 229–244.

Raw, A. 1997. Avian predation on individual neotropical social wasps (Hymenoptera, Vespidae) outside their nest. Ornitología Neotropical 8:89–92.

Remsen Jr., J. V., M. Hyde, and A. Chapman. 1993. The diets of neotropical trogons, motmots, barbets and toucans. Condor 95:178–192.

Ridgely, R. and P. Greenfield. 2001. The birds of Ecuador. Cornell University Press, Ithaca, New York, USA.

Ridgely, R. and J. Gwynne. 1989. A guide to the birds of Panama. Princeton University Press, Princeton, New Jersey, USA.

Savage, J. 2002. The amphibians and reptiles of Costa Rica: a herpetofauna between two continents, between two seas. University of Chicago Press, Chicago, Illinois, USA.

Skutch, A. 1944. Barn Swallow in Costa Rica in July. Auk 61:470–471.

Skutch, A. 1945. Life history of the Blue-throated Green Motmot. Auk 62:489–517.

Skutch, A. 1947. Life history of the Turquoise-browed Motmot. Auk 64:201–217.

Skutch, A. 1964. Life history of the Blue-diademed Motmot *Momotus momota*. Ibis 106:321–332.

Skutch, A. 1971. Life history of the Broad-billed Motmot with notes on the Rufous Motmot. Wilson Bulletin 83:74–94.

Skutch, A. 1983. Birds of tropical America. University of Texas Press, Austin, USA.

Stiles, G. and A. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

Stotz, D., J. Fitzpatrick, T. Parker, and D. Moskovitz. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Winkler, H. and D. A. Christie. 2002. Family Picidae (woodpeckers). Pages 296–555 *in* Handbook of the birds of the world. Volume 7. Jacamars to woodpeckers (J. del Hoyo, A. Elliot, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

The Wilson Journal of Ornithology 120(1):217–221, 2008

Anvil Use by the Red-cockaded Woodpecker

Kristin J. Bondo,[1,2] Lauren N. Gilson,[1] and Reed Bowman[1,3]

ABSTRACT.—We observed Red-cockaded Woodpeckers (*Picoides borealis*) wedging longleaf pine (*Pinus palustris*) seeds into crevices in tree bark in Polk County, Florida from October to December 2004. Five individuals, four uniquely color-banded and one unidentified individual, wedged ~14 seeds. Initially, we thought the birds were caching the seeds. Additional observations indicated the seeds were being wedged under the ends of the flaking bark of longleaf pines so seeds could be held firm and opened for consumption. Anvil use, where items are wedged for subsequent manipulation, is known to occur in several avian taxa, but most notably in Piciformes, Corvidae, Passerida, and Sittidae. At least 16 woodpeckers worldwide have been reported using anvils. This is the first report of Red-cockaded Woodpeckers using longleaf pine bark as an anvil to facilitate extracting the seed. *Received 29 January 2007. Accepted 22 May 2007.*

Many species of woodpeckers wedge food items too large or hard to consume whole in tree forks, crevices, or similar structures so they can be hammered or broken into smaller pieces for consumption (Winkler et al. 1995). These sites are referred to as "anvils". Anvils are classified into three types: (1) occasional anvils—any hard surface (such as a rock or flat surface) where a food item is hammered, (2) proto-anvils—any natural crevice where a food item is wedged and held firm for hammering, and (3) true anvils—anvils created by the bird in vertical branches or trunks to hold food items for consumption (Cramp 1985). Anvils also can be classified by their frequency of use: ancillary anvils are usually used opportunistically and only once, whereas main anvils are used regularly and frequently (Kedra and Mazgajski 2001).

Anvil use has been described for over 50 bird species in 12 different taxa (Sibson 1974, Winkler et al. 1995, Lefebvre et al. 2002); occasional and proto-anvil use appears to occur most frequently in Piciformes, Corvidae, Passerida, and Sittidae. Anvils often are reused in species specializing in one abundant food source (Cramp 1985). The Great Spotted Woodpecker (*Dendrocopos major*) consumes primarily conifer seeds in winter (Cramp 1985) and depends on anvils to extract seeds from thousands of cones (Winkler et al. 1995). Corvids feeding extensively on pine seeds, including the Pinyon Jay (*Gymnorhinus cyanocephalus*) (Balda 2002) and Clark's Nutcracker (*Nucifraga columbiana*) (Tomback 1998), wedge entire cones into anvils to extract the seeds. The Pinyon Jay often re-uses anvils (Balda 2002), but these are proto-anvils and not true anvils as used by the Great Spotted Woodpecker.

Proto-anvils are used to open individual winged pine seeds for consumption. Winged pine seeds are similar in appearance to the samaras of ash (*Fraxinus*) and maple (*Acer*). The seed is on one end and a thin papery wing encases the seed and extends beyond the seed. White-headed Woodpeckers (*Picoides albolarvatus*) (Garrett et al. 1996), Brown-headed Nuthatches (*Sitta pusilla*) (Morse 1967, 1968), White-breasted Nuthatches (*S. carolinensis*) (Morse 1968), Pygmy Nuthatches (*S. pygmaea*) (Norris 1958), and Pine Warblers (*Dendroica pinus*) (Morse 1967) wedge winged pine seeds into bark or a crevice to extract the seed. Hairy Woodpeckers (*Picoides villosus*) consume winged pine seeds by wedging them into ponderosa pine (*Pinus ponderosa*) cones and using the cones as anvils to extract the seeds (Stallcup 1969).

Conner et al. (2001) described the seed handling behavior of the Red-cockaded Woodpecker (*Picoides borealis*). The seed is placed between the trunk and the bird's breast before the seed wing is detached and the seed eaten; however, neither Conner et al. (2001) nor previous authors mention use of anvils. The ob-

[1] Archbold Biological Station, P. O. Box 2057, Lake Placid, FL 33862, USA.

[2] Current address: University of Regina, Department of Biology, Regina, SK S4S 0A2, Canada.

[3] Corresponding author; e-mail: rbowman@archbold-station.org

jective of this paper is to describe anvil use by Red-cockaded Woodpeckers.

OBSERVATIONS

Observations were made of five individual birds in two different family groups. Both territories occurred in mesic longleaf pine (*Pinus palustris*) forests in Polk County, south-central Florida at the Avon Park Air Force Range (APAFR) (27° 38′ N, 81° 17′ W). As part of a long-term study, all individuals in the population are uniquely color-banded and the gender, social, and nesting status of all birds are known (Bowman et al. 1999, 2004). We conducted observations in the mornings and evenings while monitoring the population throughout September 2004–March 2005. We (KJB) observed handling and consumption of pine seeds from October to December.

The breeding female from one family group, consisting of a male and female breeding pair, emerged from her roost at 0740 hrs EST on 24 October, followed shortly by her mate which was roosting nearby. One bird of the pair, whose identity was unconfirmed because of the similarity of the pair's color-band combinations, landed on the underside of a longleaf pine cone. It removed a winged seed from the opened pine cone, flew to the trunk of the same tree, and ascended ~2 m by circling the bole to a total height of 5–7 m. It then wedged the winged seed vertically behind loose bark and began to peck. While this bird was handling its seed, its mate flew to the same cone, removed another winged seed, flew and climbed to a position above and opposite its mate on the same tree, and performed the same behavior. Following wedging and pecking at each seed, both birds returned to this same cone for subsequent seeds even though the tree bore many cones. In each instance the woodpeckers landed on the cone, one at a time, returned to the tree bole wedging each seed vertically behind loose bark and followed the seed insertion behavior by pecking. In total, the two birds removed and handled seven seeds in the same manner.

Initially we thought the birds were caching seeds because after the birds pecked, presumably to remove the seed from the wing, we did not observe any seed wings fall to the ground. In addition, the birds did not immediately wedge the seed, but circled up and around the bole, presumably searching for a suitable place to cache the seed. We later observed additional seed-wedging behavior by other Red-cockaded Woodpeckers and confirmed that seeds were being wedged to aid in handling and consumption. The bark was used as an "anvil" to facilitate the detachment of the non-edible wing from the seed.

We encountered a female fledgling in another family group on 30 November at 0719 hrs EST perched on a longleaf pine cone ~2 m above ground. The cone was on a partially uprooted but still living longleaf pine tree that had recently been blown over. She removed a winged seed from the cone, flew to the trunk of another longleaf pine and carried the seed to the side opposite from where we were standing, ~1.5 m above ground. Before we could again observe the bird, she had flown away. We found three longleaf pine seeds wedged firmly under the bark on the trunk of the tree where we saw her take the seed. In all cases, the seed had been removed and the remaining portion wedged vertically in the bark with the end formerly containing the seed facing up and the wing facing down.

We also observed the breeding male at this territory handle four longleaf pine seeds on two different occasions between early November and early December. Each time, the male removed the seed from a cone, flew with it to the upper trunk or a vertical branch where the bark was visibly peeling, wedged it behind bark, and pecked. We observed a bird from this same territory on 4 November, whose color-band combination was not observed, handle two pine seeds in the same manner. Each bird returned to obtain more seeds from the same cone in all instances. We concluded the seeds had been consumed and this behavior represented "anvil" use rather than caching.

DISCUSSION

Occasional and proto-anvil use has been recorded in many avian taxa worldwide (Lefebrve et al. 2002), and we summarized use of proto-anvils in 16 species of woodpeckers worldwide (Table 1). Only one woodpecker species, the Great Spotted Woodpecker, uses true anvils and frequently re-uses them (Winkler et al. 1995). Our observations of Red-cockaded Woodpeckers in Florida suggest use of proto-anvils rather than true anvils. The

TABLE 1. Woodpeckers (Picidae) documented to use proto-anvils.

Taxa	Species	Anvil location	Food items
Melanerpes lewis[a]	Lewis's	Cleft in snag or power pole	Acorns, nuts
M. erythrocephalus	Red-headed	Cleft in branch,[b,c,d] power pole[c]	Acorns,[b,d] insects[c]
M. formicivorus[e,f]	Acorn	Cleft in limb	Acorns
M. flavifrons[g]	Yellow-fronted	Base of broken limb	Insects, fruits
M. hypopolius[h]	Gray-breasted	Clefts, excavated holes	Insects, fruits
M. carolinus	Red-bellied	Cleft in bark,[i] tree[j,k] or post[k]	Seeds,[i,j] nuts[k]
Sphyrapicus varius[l]	Yellow-bellied Sapsucker	Cleft in bark	Seeds
Dendrocopos minor[m]	Lesser Spotted	Cleft in bark	Cones, nuts
D. medius[m]	Middle Spotted	Cleft in bark	Cones, seeds
D. leucotos[m]	White-backed	Cleft in tree	Nuts
D. major	Great Spotted	Cleft in tree,[n] poles[o]	Cones,[n,o] fruit,[m] nuts,[m] insects,[m] nestlings[m]
D. syriacus	Syrian	Cleft in wall,[p] tree,[m] or branch[q]	Fruit stones,[p,m] walnuts[m]
Picoides pubescens[r]	Downy	Cleft in bark, knotholes	Seeds
P. villosus	Hairy	Cleft in bark,[i] cones[t]	Seeds[i,t]
P. albolarvatus[s]	White-headed	Cleft in bark	Seeds
Picus viridis[q]	European Green	Cleft	Cones

[a] Bock (1970), [b] Kilham (1958), [c] Rogers et al. (1979), [d] Moskovits (1978), [e] MacRoberts (1970), [f] MacRoberts and MacRoberts (1976), [g] Oniki and Willis (1998), [h] Leonard (2000), [i] Erlwein (1996), [j] Mueller (1971), [k] Shackelford et al. (2000), [l] Labedz (1980), [m] Cramp (1985), [n] Tracy (1924), [o] Kedra and Mazgajski (2001), [p] Gorman (1998), [q] Bunyard (1924), [r] Davis (1995), [s] Garrett et al. (1996), [t] Stallcup (1969).

woodpeckers did not excavate the anvil site nor did they re-use them.

Anvil use appears to be relatively common among European woodpeckers (Winkler et al. 1995), but their use seems less common among North American woodpeckers. Whether this is a real behavioral difference, such as differences in diet, differences in forest structure that might reduce the availability of suitable anvil sites, or simply an artifact of observational or reporting biases is unknown. Despite numerous studies on Red-cockaded Woodpeckers, this behavior has not been previously reported. We do not know if this behavior is widespread and unreported, or localized to Florida or even this population. Avon Park Air Force Range is near the southern limit of longleaf pines and trees may be edaphically limited in size. We often observed Red-cockaded Woodpeckers foraging within 10–12 m of the ground but elsewhere, foraging heights might be greater and anvil use more difficult to observe. In foraging studies of Red-cockaded Woodpeckers in longleaf pine forests in Texas, woodpeckers appeared to hold seeds loosely between their breast and the bark while consuming them (R. N. Conner, pers. comm.). This might have been a misinterpretation of anvil use because, to our knowledge, neither woodpeckers nor nuthatches are known to hold food items between their breast and an object to facilitate consumption. The Great Spotted Woodpecker will hold food between breast and substrate before wedging it (Winkler et al. 1995) and most woodpeckers, particularly the Red-bellied Woodpecker (*Melanerpes carolinus*), will hunch their shoulders forward and push their belly against the bark when hammering food items so that fallen portions of their food can be trapped (Kilham 1983). Red-cockaded Woodpeckers may place seeds between breast and substrate to help position it before it is inserted vertically into the bark.

Anvil use may occur only occasionally even in Florida. The majority of the Red-cockaded Woodpecker diet consists of small arthropod prey (Jackson 1994), which are probably sufficiently small to be consumed without the use of anvils. Inclusion of winged pine seeds in the diet of Red-cockaded Woodpeckers may vary greatly, even when pine mast is plentiful (Hooper and Lennartz 1981), suggesting seed consumption may depend on

the relative availability of other foods. Use of anvils in birds may be an evolutionary precursor to caching (Richards 1958, Winkler et al. 1995), which may be adaptive if food resources vary spatially and/or temporally (Smith and Reichman 1984). Red-cockaded Woodpeckers are not known to cache food (Jackson 1994), except perhaps bone fragments (Repasky et al. 1991). Caching occurs in other woodpeckers, most notably among the *Melanerpes* species, but is not widely reported in the genus *Picoides*. Although the Hairy Woodpecker may cache rarely, it has a relative hippocampus volume similar to the scatter-hoarding Red-bellied Woodpecker (Volman et al. 1997).

Some woodpecker species use proto-anvils to break apart large or difficult to consume food items (Winkler et al. 1995) and it is likely Red-cockaded Woodpeckers use anvils in the same manner. Caching by Red-cockaded and other woodpeckers (Winkler et al. 1995) should be re-evaluated because anvil use and caching are similar behaviors that can be difficult to distinguish (Winkler et al. 1995). Future research should address the frequency of anvil use and re-use among woodpeckers, and distinguish those observations from caching. The evolutionary relationship between anvil use and caching within woodpeckers and, specifically within the genus *Picoides*, warrants further study.

ACKNOWLEDGMENTS

We thank Archbold Biological Station and Avon Park Air Force Range for funding and support. We also thank the University of Regina library, J. B. Dunning, and H. P. Weeks for help obtaining inter-library loans, and R. J. Fisher, R. N. Conner, and D. C. Rudolph for helpful comments improving the manuscript. We are indebted to the O'Hanlons for providing hospitality and moral support, and C. Rook-Hobbs, who expedited the manuscript's completion.

LITERATURE CITED

Balda, R. P. 2002. Pinyon Jay (*Gymnorhinus cyanocephalus*). The birds of North America. Number 605.

Bock, C. E. 1970. The ecology and behavior of the Lewis's Woodpecker (*Asyndesmus lewis*). University of California Publications in Zoology 92:1–100.

Bowman, R., D. L. Leonard Jr., L. K. Backus, and A. R. Mains. 1999. Interspecific interactions with foraging Red-cockaded Woodpeckers in south-central Florida. Wilson Bulletin 111:346–353.

Bowman, R., D. L. Leonard Jr., D. Swan, and D. Schwalm. 2004. Demography and population trends of a small Red-cockaded Woodpecker population in south-central Florida. Pages 187–197 *in* Red-cockaded Woodpecker: road to recovery (R. Costa and S. J. Daniels, Editors). Hancock House Publishers, Blaine, Washington, USA.

Bunyard, P. F. 1924. Surry field notes. British Birds 17:202.

Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. Red-cockaded Woodpecker. Surviving in a fire maintained ecosystem. University of Texas Press, Austin, USA.

Cramp, S. 1985. The birds of the Western Palearctic. Volume 4. Oxford University Press, New York, USA.

Davis Jr., W. E. 1995. Downy Woodpecker and White-breasted Nuthatch use "vice" to open sunflower seeds: is this an example of tool use? Bird Observer 23:339–342.

Erlwein, K. M. 1996. Hairy and Red-bellied woodpeckers use bark crevice to break open seeds. Kingbird 46:200–201.

Garrett, K. L., M. G. Raphael, and R. D. Dixon. 1996. White-headed Woodpecker (*Picoides albolarvatus*). The birds of North America. Number 252.

Gorman, G. 1998. Syrian Woodpecker using wall crevice as "anvil". British Birds 91:378.

Hooper, R. G. and M. R. Lennartz. 1981. Foraging behavior of the Red-cockaded Woodpecker in South Carolina. Auk 98:321–334.

Jackson, J. A. 1994. Red-cockaded Woodpecker (*Picoides borealis*). The birds of North America. Number 85.

Kedra, A. H. and T. D. Mazgajski. 2001. Factors affecting anvil utilization by Great Spotted Woodpecker *Dendrocopos major*. Polish Journal of Ecology 49:79–86.

Kilham, L. 1958. Sealed-in winter stores of Red-headed Woodpeckers. Wilson Bulletin 70:107–113.

Kilham, L. 1983. Life history studies of woodpeckers of eastern North America. Publications of the Nuttall Ornithological Club Number 20.

Labedz, T. E. 1980. Yellow-bellied Sapsucker feeding on hackberry seeds. Nebraska Bird Review 48:89.

Lefebvre, L., N. Nicolakakis, and D. Boire. 2002. Tools and brains in birds. Behaviour 139:939–973.

Leonard Jr., D. L. 2000. Breeding and life history observations of the Gray-breasted Woodpecker (*Melanerpes hypopolius*). Ornitología Neotropical 11:341–348.

MacRoberts, M. H. 1970. Notes on the food habits and food defense of the Acorn Woodpecker. Condor 72:196–204.

MacRoberts, M. H. and B. R. MacRoberts. 1976. Social organization and behavior of the Acorn

Woodpecker in central coastal California. Ornithological Monographs 21:1–115.

Morse, D. H. 1967. Foraging relationships of Brown-headed Nuthatches and Pine Warblers. Ecology 48:94–103.

Morse, D. H. 1968. The use of tools by Brown-headed Nuthatches. Wilson Bulletin 80:220–224.

Moskovits, D. 1978. Winter territorial and foraging behavior of Red-headed Woodpeckers in Florida. Wilson Bulletin 90:521–535.

Mueller, H. C. 1971. Sunflower seed carrying by Red-bellied Woodpeckers (*Centurus carolinus*). Bird-Banding 42:46–47.

Norris, R. A. 1958. Comparative biosystematics and life history of the nuthatches *Sitta pygmaea* and *Sitta pusilla*. University of California Publications in Zoology 56:119–300.

Oniki, Y. and E. O. Willis. 1998. Nesting of Yellow-fronted Woodpeckers *Melanerpes flavifrons* (Picidae). Ornitología Neotropical 9:81–86.

Repasky, R. R., R. J. Blue, and P. D. Doerr. 1991. Laying Red-cockaded Woodpeckers cache bone fragments. Condor 93:458–461.

Richards, T. J. 1958. Concealment and recovery of food by birds, with some relevant observations on squirrels. British Birds 51:497–508.

Rogers, D. T., J. A. Jackson, B. J. Schardien, and M. S. Rogers. 1979. Observations at a nest of a partial albino Red-headed Woodpecker. Auk 96: 206–207.

Shackelford, C. E., R. E. Brown, and R. N. Conner. 2000. Red-bellied Woodpecker (*Melanerpes carolinus*). The birds of North America. Number 500.

Sibson, R. B. 1974. Rock Wren using an anvil. Notornis 21:305.

Smith, C. C. and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics 15:329–351.

Stallcup, P. L. 1969. Hairy Woodpeckers feeding on pine seeds. Auk 86:134–135.

Tomback, D. F. 1998. Clark's Nutcracker (*Nucifraga columbiana*). The birds of North America. Number 331.

Tracy, N. 1924. Woodpeckers and pine-cones. British Birds 17:276–279.

Volman, S. F., T. C. Grubb Jr., and K. C. Schuett. 1997. Relative hippocampal volume in relation to food-storing behavior in four species of woodpecker. Brain Behavioral Evolution 409:110–120.

Winkler, H., D. A. Christie, and D. Nurney. 1995. Woodpeckers. An identification guide to the woodpeckers of the world. Houghton Mifflin Company, New York, USA.

The Wilson Journal of Ornithology 120(1):221–225, 2008

Gender Identification of Grasshopper Sparrows Comparing Behavioral, Morphological, and Molecular Techniques

Frank K. Ammer,[1,4,5] Petra Bohall Wood,[2] and Roger J. McPherson[3]

ABSTRACT.—Correct gender identification in monomorphic species is often difficult especially if males and females do not display obvious behavioral and breeding differences. We compared gender specific morphology and behavior with recently developed DNA techniques for gender identification in the monomorphic Grasshopper Sparrow (*Ammodramus savannarum*). Gender was ascertained with DNA in 213 individuals using the 2550F/2718R primer set and 3% agarose gel electrophoresis. Field observations using behavior and breeding characteristics to identify gender matched DNA analyses with 100% accuracy for adult males and females. Gender was identified with DNA for all captured juveniles that did not display gender specific traits or behaviors in the field. The molecular techniques used offered a high level of accuracy and may be useful in studies of dispersal mechanisms and winter assemblage composition in monomorphic species. *Received 8 January 2007. Accepted 17 June 2007.*

[1] West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry and Natural Resources, West Virginia University, P. O. Box 6125, Morgantown, WV 26506, USA.

[2] U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry and Natural Resources, West Virginia University, P. O. Box 6125, Morgantown, WV 26506, USA.

[3] Department of Biology, Clarion University of Pennsylvania, Clarion, PA 16214, USA.

[4] Current address: Department of Biology, Frostburg State University, 101 Braddock Road, Frostburg, MD 21532, USA.

[5] Corresponding author; e-mail: fammer@frostburg.edu

Gender identification of adult and juvenile birds is often difficult in demographic studies

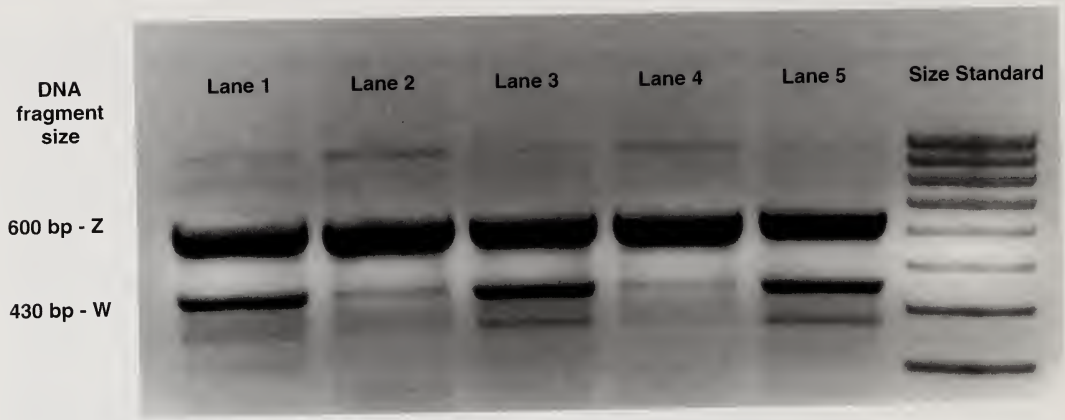


FIG. 1. Gender typing of Grasshopper Sparrows using PCR methods; 3% agarose gel showing gene products amplified with the Fridolfsson and Ellegren (1999) 2550F/2718R primers. Lanes 1, 3, and 5 represent the typical 600 bp and 430 bp band patterns of females. Lanes 2 and 4 represent the typical 600 bp band pattern of males. The size standard lane represents a 100 bp DNA ladder.

examining species with subtle or no dimorphic characters. Gender can be reliably ascertained only during the breeding season when behavioral and external sex characteristics can be directly observed in species lacking size or plumage dimorphism (Underwood et al. 2002). Identifying the gender of juveniles presents additional difficulties as these individuals display no gender related traits or behaviors. The ability to assign gender is especially useful when examining sex-specific factors such as juvenile sex ratios and gender specific habitat selection (Underwood et al. 2002).

The most reliable methods to identify gender until recently relied on invasive surgical procedures that require anesthesia and are not a feasible option for most field studies. The introduction of polymerase chain reaction (PCR) techniques targeting the chromo-helicase DNA (CHD) binding gene (Griffiths et al. 1998, Fridolfsson and Ellegren 2000) provides a noninvasive alternative. The avian *CHD-W* and *CHD-Z* genes occur on different sex chromosomes and gender can be ascertained by examining the composition of these genes (Boutette et al. 2002). Recently developed techniques rely on PCR primers that anneal to specific conserved exonic regions and amplify across an intron in both genes (Griffiths et al. 1998, Fridolfsson and Ellegren 1999, Dawson et al. 2001). This technique is based on noncoding introns in the *CHD-Z* and *CHD-W* genes which vary in length and therefore can be differentiated by gel electrophoresis (Griffiths et al. 1998).

The Grasshopper Sparrow (*Ammodramus savannarum*) is a widely distributed North American grassland species that has shown long-term population declines over much of its range (Brennan and Kuvlesky 2005). Individuals of the eastern subspecies (*A. s. pratensis*) display no plumage or size dimorphism making it extremely difficult to identify gender by observation alone. Further, adult females in breeding territories are secretive and commonly spend substantial time on the ground walking to and from the nest area, making it difficult to observe female-specific brooding and feeding behaviors (Vickery 1996). Territorial male behaviors are more obvious because they commonly perch and sing at the periphery of their territory (Vickery 1996). Some morphological and behavioral characteristics may be useful in gender identification in this species; however, quantitative evidence supporting the accuracy and applicability of these characters is lacking (Delany et al. 1994).

We examined the effectiveness of the 2550F/2718R (Fridolfsson and Ellegren 1999) primer set for gender identification of adult and juvenile Grasshopper Sparrows. We then used molecular gender results to compare with morphological characters and breeding behavior to examine their efficacy for accurate gender assessment in the field.

TABLE 1. Morphological characteristics of Grasshopper Sparrows captured in southwestern West Virginia, 2002. *= significant differences.

Gender	*n*	Mass (g)			Wing chord (mm)			Tarsus length (mm)			Bill width (mm)			Bill length (mm)		
		Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Juvenile																
Male	34	14.7	0.30	11.0–18.0	51.5	1.51	34.0–64.0	23.6	0.14	22–25	5.27	0.15	3.5–6.3	6.39	0.25	4.0–8.1
Female	15	14.0	0.60	9.0–17.0	47.3	2.69	27.0–59.0	23.6	0.21	22–25	5.15	0.29	3.3–6.4	6.09	0.43	3.5–8.0
Adult																
Male	131	17.3	0.07	15.0–20.0	62.5*	0.17	57.5–67.0	24.7	0.13	19–27	6.28*	0.03	3.5–6.8	8.06*	0.03	7.1–8.9
Female	31	17.3	0.26	14.5–22.0	59.3*	0.19	57.0–62.0	24.6	0.76	23–25	6.03*	0.05	5.5–6.5	7.90*	0.06	7.3–8.7

METHODS

Field Methods.—We captured 213 Grasshopper Sparrows during the 2002 breeding season from six study plots encompassing ~503 ha of reclaimed grassland on three mountaintop mine complexes in Boone, Logan, Kanawha, and Fayette counties in southwestern West Virginia. Birds were captured with mist nets using conspecific song playback from April to August. Captured individuals were banded with U.S. Geological Survey (USGS) leg bands and a unique combination of two colored plastic leg bands for future visual identification. Mass, wing chord, bill width, bill length, and tarsus length were measured following Pyle et al. (1997). Gender and age of captured individuals were assigned in the field using behavioral observations, plumage differences (age), physical measurements, and breeding characteristics (cloacal protuberance and brood patch) (Pyle et al. 1997). When possible, juveniles were captured and processed prior to fledging (5–6 days post hatch) and banded with a USGS leg band and a single colored leg band.

Approximately 50 μl of blood was collected from adult and juvenile Grasshopper Sparrows by femoral veinipuncture. Blood samples were stored in 1 ml of a standard blood lysis buffer (Seutin et al. 1990) at 4° C. Care was taken to ensure that bleeding had stopped prior to release. All individuals were released at the capture site immediately following sampling.

DNA Isolation and Polymerase Chain Reaction Amplification.—Genomic DNA was isolated using a DNeasy Tissue Kit (QIAGEN Inc., Valencia, CA, USA) following the manufacturers protocol for blood and stored at 4° C. Mention of tradenames or commercial products does not constitute endorsement or recommendation of use by the U.S. Government. Spectrophotometric analysis was performed on each sample to quantify yield and ensure proper DNA concentrations necessary for amplification by PCR. A portion of the CHD gene was amplified using modified methods of Fridolfsson and Ellegren (1999) and Dawson et al. (2001). Briefly, reactions were conducted in 10 μl volumes using 1 μM of each primer, and 200 μM of each dNTP, 2.0 mM $MgCl_2$, 1× PCR reaction buffer, 50 ng of genomic DNA template, and 0.25 units

TABLE 2. Gender classification results for Grasshopper Sparrows captured in 2002 in southwestern West Virginia based on parametric quadratic discriminant function analyses and error rates based on cross validation. Wing chord, bill width, and bill length were included as criterion variables in the discriminant analysis. Values are number of individuals (*n*) and the percent (%) classified correctly into each gender.

		Adult			Juvenile		
		Predicted female	Predicted male	Actual gender	Predicted female	Predicted male	Actual gender
Female	*n*	27	4	31	11	4	15
	%	87.1	12.9		73.3	26.7	
Male	*n*	29	100	129	11	23	34
	%	22.5	77.5		32.4	67.6	

of *Taq* polymerase (New England BioLabs Inc., Ipswich, MA, USA).

The thermal profile began with an initial denature at 94° C for 2 min. A touchdown procedure was performed as follows: (1) preheat 94° C for 2 min; (2) 10 cycles of denaturation, 94° C for 45 sec, annealing 60° C–51° C (−1° C per cycle) for 45 sec, extension, 72° C for 45 sec; (3) 30 cycles denaturation, 94° C for 30 sec, annealing, 50° C for 30 sec, extension, 72° C for 30 sec; and (4) extend at 72° C for 10 min and stored at 4° C. All thermal cycling was performed in a DNA Engine (PTC 200, Bio-Rad Laboratories Inc. Hercules, CA, USA) configured with a heated lid. PCR products were visualized on 3% agarose gels stained with ethidium bromide (Fig. 1). Females had two bands (ZW) while males had one (ZZ). Random samples were electrophoresed on 6% polyacrylamide gel stained with ethidium bromide to ensure adequate resolution was obtained with agarose.

Statistical Analysis.—Analyses were conducted using the SAS software package (SAS Institute Inc. 1999). Morphological characters were tested independently for differences between adult males and females, and between juvenile males and females with analysis of variance (ANOVA) (Zar 1996). Mass, wing chord, bill width, bill length, and tarsus length were the dependent variables in the models. Differences were considered significant at $\alpha = 0.10$. Morphological characters with $P \leq 0.10$ were included as criterion variables in parametric quadratic discriminant function analyses (DISCRIM) to assign adult and juvenile individuals into gender classes (SAS Institute Inc. 1999). Error rates were based on cross validation procedures.

RESULTS

We identified gender using molecular techniques for all 164 adults sampled. Gender assignments based on data collected in the field using breeding characteristics and behaviors were 100% consistent with DNA analyses. Gender assignment using morphological data was less consistent. For adults, wing chord ($F_{1,153} = 40.5$, $P < 0.001$), bill width ($F_{1,115} = 32.2$, $P < 0.001$), and bill length ($F_{1,152} = 2.80$, $P = 0.10$) differed by gender, while mass ($F_{1,153} = 1.73$, $P = 0.19$) and tarsus length ($F_{1,151} = 0.19$, $P = 0.67$) did not (Table 1). Discriminant function analysis with bill width, bill length, and wing chord correctly classified 87.1% of adult females and 77.5% of adult males to the gender groups previously ascertained with molecular and behavioral techniques (Table 2).

We successfully assigned gender using molecular techniques to all 49 juveniles/nonbreeders sampled in 2002. These 34 males and 15 females did not display sex related traits or behaviors in the field and gender could not be assigned based on behavioral data. No morphological differences were detected between genders in juveniles with univariate analyses (mass: $F_{1,42} = 1.38$, df = 1, $P = 0.25$, wing chord: $F_{1,42} = 2.06$, df = 1, $P = 0.16$, bill width: $F_{1,39} = 0.05$, df = 1, $P = 0.83$, bill length: $F_{1,42} = 0.37$, df = 1, $P = 0.55$, and tarsus length: $F_{1,42} = 0.01$, df = 1, $P = 0.93$). However, discriminant function analysis using bill width, bill length, and wing chord as criterion variables correctly assigned 73.3% of females and 67.6% of males (Table 2).

DISCUSSION

Molecular gender assignment for adult Grasshopper Sparrows using methods of Fri-

dolfsson and Ellegren (1999) was in 100% agreement with behavioral data collected in the field. Gender assignment with this technique was an excellent alternative to more invasive procedures normally required to assign gender in juveniles. The gender of adults displaying territorial behavior and external characters was reliably identified in all individuals examined in the field. However, if gender discrimination is not conclusive with breeding characters and behaviors, we suggest using adult wing chord, bill width, and bill length to assist gender identification in the field. These three measurements were 87% accurate in assigning females and 78% accurate for assigning males.

Gender identification of juveniles not displaying secondary sexual characteristics and behaviors remains a challenge for researchers in the field. Discrimination of juvenile gender using morphological characters was less accurate than for adults in breeding condition. Significant differences in morphometrics between juveniles and adults were not surprising because a large percentage (86%) of the juveniles sampled were 5–6 day old nestlings and fledglings not yet fully developed.

The molecular techniques used were efficient, relatively inexpensive, and less invasive than traditional procedures. These methods do not require extensive training and may be performed in many modestly equipped laboratories. Data obtained with these techniques may be instrumental in providing answers to questions targeting dispersal mechanisms and winter assemblage composition in monomorphic species.

ACKNOWLEDGMENTS

We thank those individuals who provided assistance with data collection and analyses, especially George Seidel, Joshua Scullen, Danielle Mortensen, Scott Bosworth, Amanda Carroll, Nick Ammer, and Amanda Ammer. The Environmental Protection Agency, West Virginia Division of Natural Resources, U.S. Geological Survey, West Virginia University Research Corporation, WVU Division of Forestry, and the USGS West Virginia Cooperative Fish and Wildlife Research Unit provided financial, administrative, and logistic support. Arch Coal Inc., Cannelton Mine, Amherst Corporation, and the Ark Land Company provided logistic support, access to field sites, and field housing. Gregory Forcey, Michael Capp, Dusty Perkins, and an anonymous reviewer provided valuable comments on earlier versions of this manuscript.

LITERATURE CITED

Boutette, J. B., E. C. Ramsay, L. N. D. Potgieter, and S. A. Kania. 2002. An improved polymerase chain reaction-restriction fragment length polymorphism assay for gender identification in birds. Journal of Avian Medicine and Surgery 16:198–202.

Brennan, L. A. and W. P. Kuvlesky. 2005. North American grassland birds: an unfolding crisis? Journal of Wildlife Management 69:1–13.

Dawson, D. A., S. Darby, F. M. Hunter, A. P. Krupa, I. L. Jones, and T. Burke. 2001. A critique of avian CHD-based molecular sexing protocols illustrated by a Z-chromosome polymorphism detected in auklets. Molecular Ecology Notes 1:201–204.

Delany, M. F., C. T. Moore, and D. R. Progulske Jr. 1994. Distinguishing gender of Florida Grasshopper Sparrows using body measurements. Florida Field Naturalist 22:48–51.

Fridolfsson, A. K. and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30:116–121.

Fridolfsson, A. K. and H. Ellegren. 2000. Molecular evolution of the avian CHD1 genes on the Z and W sex chromosomes. Genetics 155:1903–1912.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Pyle, P., S. N. G. Howell, D. F. DeSante, R. P. Yunick, and M. Gustafson. 1997. Identification guide to North American birds. Part 1. Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, USA.

SAS Institute Inc. 1999. SAS/STAT user's guide. SAS Institute Inc., Cary, North Carolina, USA.

Seutin, G., B. N. White, and P. T. Boag. 1990. Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoology 69: 82–90.

Underwood, R. M., R. J. Crockett, R. R. Roth, C. L. Keeler Jr., and M. S. Parcells. 2002. A comparison of flow cytometry and the polymerase chain reaction as sexing techniques for the Wood Thrush. Journal of Field Ornithology 73:239–245.

Vickery, P. D. 1996. Grasshopper Sparrows (*Ammodramus savannarum*). The birds of North America. Number 239.

Zar, J. H. 1996. Biostatistical analysis. Third Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

The Wilson Journal of Ornithology 120(1):226–228, 2008

Abnormal Eggs of Rio Grande Wild Turkeys on the Edwards Plateau, Texas

Kyle B. Melton,[1] Justin Z. Dreibelbis,[1] Ray Aguirre,[2] Bret A. Collier,[1,4] T. Wayne Schwertner,[3] Markus J. Peterson,[1] and Nova J. Silvy[1]

ABSTRACT.—We studied the reproductive ecology of Rio Grande Wild Turkeys (*Meleagris gallopavo intermedia*) in the Edwards Plateau region, Texas during 2005 and 2006. Runt eggs from a single adult female were observed through three nesting events over 2 years. Mean mass and volume for the runt eggs were 44% of normal Wild Turkey eggs. Production of runt eggs is common in domesticated gallinaceous birds, yet little information is available on runt egg production in wild gallinaceous birds. To our knowledge, our observations are the first which indicate runt egg production occurs in Wild Turkeys. *Received 20 February 2007. Accepted 11 May 2007.*

Knowledge of reproductive rates is critical to monitoring long-term dynamics of Wild Turkey (*Meleagris gallopavo*) populations (Vangilder 1992). Reproductive rates are influenced by multiple components of the reproductive process. Runt eggs, those having volumes <75% of the average (Koenig 1980), are perhaps the most common egg abnormality documented in domestic fowl (Pearl and Curtis 1916, Romanoff and Romanoff 1949). Several avian species, both domestic and wild, have been known to produce runt eggs (Hernandez et al. 2006), but occurrence is low for most species; approximately one in every 1,000–2,000 eggs (Mallory et al. 2004, Hernandez et al. 2006). Documentation of runt eggs in wild populations is rare (Rothstein 1973, Mallory et al. 2004). Our objective is to report what we believe is the first observation of runt egg production by Wild Turkeys.

[1] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA.

[2] Texas Parks and Wildlife Department, Comfort, TX 78013, USA.

[3] Texas Parks and Wildlife Department, Mason, TX 76856, USA.

[4] Corresponding author; e-mail: bret@tamu.edu

OBSERVATIONS

We tracked, via triangulation and homing (White and Garrott 1990), 11 radio-marked Wild Turkey hens through two nesting seasons (2005–2006) on a 984-ha ranch ~9.5-km north of Leakey, Texas, USA. One of these radio-marked hens produced runt eggs during three consecutive nesting attempts (2 in 2005, 1 in 2006). We captured this 3.7-kg hen on 24 February 2004 as an adult (≥18 months of age). She produced a clutch of five eggs in 2004 with no abnormal appearing eggs.

We first observed a set of runt eggs on 13 April 2005 during the hen's initial 2005 nesting attempt. The first nest contained three runt eggs and one normal egg. Normal laying behavior for turkeys is to lay one egg per day (Healy 1992). Daily checks when the hen was off the nest confirmed that no additional eggs were laid until 18 April when one additional runt egg was laid (total clutch; four runt eggs, one normal egg). We continued to monitor the nest daily from 18 to 27 April during which time we did not locate the hen on the nest although she was located in the nest area. We observed one additional runt egg, on 28 April, bringing the clutch size to six (five runt eggs and one normal egg). One additional runt egg was deposited between 28 April and 1 May bringing the total clutch to seven (six runt eggs and one normal egg). The normal-sized egg was depredated on 2 May and only six runt eggs remained. We considered the nest depredated on 4 May when the remaining eggs were found hidden under leaf litter (undamaged) in separate locations away from the nest. We collected the runt eggs, measured size and volume, and ascertained if they were viable.

We continued to radio-track the hen and documented a second nesting attempt on 30 May 2005 containing three runt eggs. During

TABLE 1. Characteristics of normal and runt Rio Grande Wild Turkey eggs on the Edwards Plateau, Texas, 2005–2006.

	n	Min	Max	Mean	SD
Normal					
Length, mm	176	53.4	65.6	61.0	0.19
Width, mm	176	40.7	72.0	47.1	0.24
Weight, g	176	47.4	85.1	68.7	6.46
Volume, ml	161	27.5	55.0	43.6	4.62
Runt					
Length, mm	7	39.2	49.5	44.7	0.39
Width, mm	7	33.4	37.5	35.5	0.17
Weight, g	7	23.6	34.2	30.3	3.79
Volume, ml	4	16.5	22.0	19.3	3.18

monitoring of the renesting attempt, the hen abandoned the nest. Within 1 week she was located >1 km from the nest and was not observed near the nest again. We collected the three runt eggs on 9 June 2005 to check viability and to obtain measurements. We documented a third nest the following year by this hen on 19 April 2006, which contained 12 runt eggs and four normal eggs. We monitored the nest and hen daily through 14 days of incubation, and found the nest partly depredated on 3 May 2006. We collected shell remains from 10 depredated eggs (eight runt and two normal eggs).

We located 90 nests from 69 individual hens during 2005–2006 and obtained clutch sizes for 70 nests (n = 885 eggs). Based on our data, runt eggs in Wild Turkeys occurred at a frequency of 2.4% (21/885). We measured length (mm), width (mm), mass (g), and volume (ml) using water displacement for undamaged runt eggs (n = 7) and undamaged/unhatched normal eggs (n = 176) collected during 2005–2006 (Table 1). Mean mass and volume of the runt eggs was 44% of normal eggs; 31% smaller than the suggested size for classifying eggs as runts (Koenig 1980). None of the runt eggs contained yolks, making them unviable.

DISCUSSION

Production of runt eggs is usually thought to be caused by a temporary disturbance to the reproductive system (Pearl and Curtis 1916, Romanoff and Romanoff 1949). Moreover, birds under environmental stress may be more prone to produce runt eggs (Mallory et al. 2004). Wild Turkey reproduction and, therefore, egg production is negatively affected by low rainfall and soil moisture (Beasom and Pattee 1980) as well as nutritional limitation (Blankenship 1992). Continued production of runt eggs suggests a congenital defect or permanent injury to the bird's oviduct (Pearl and Curtis 1916, Mulvihill 1987). The frequency of runt eggs in Wild Turkeys is low; persisting environmental stresses presumably could alter their frequency and reduce the potential production of the population. However, the low prevalence of runt eggs in our study suggests the impact of runt egg production on population trajectory is probably limited.

ACKNOWLEDGMENTS

Funding was provided by the Texas Turkey Stamp Fund through the Texas Parks and Wildlife Department, the National Wild Turkey Federation Texas State Superfund, and the Department of Wildlife and Fisheries Sciences, Texas A&M University. This research was conducted under Texas A&M University Animal Use Permit 2005-005.

LITERATURE CITED

Beasom, S. L. and O. H. Pattee. 1980. The effect of selected climatic variables on Wild Turkey productivity. Proceedings of the National Wild Turkey Symposium 4:127–135.

Blankenship, L. H. 1992. Physiology. Pages 84–100 *in* The Wild Turkey: biology and management (J. G. Dickson, Editor). Stackpole Books, Harrisburg, Pennsylvania, USA.

Healy, W. M. 1992. Behavior. Pages 46–65 *in* The Wild Turkey: biology and management (J. G. Dickson, Editor). Stackpole Books, Harrisburg, Pennsylvania, USA.

Hernandez, F., J. A. Arredondo, F. Hernandez, F. C. Bryant, and L. A. Brennan. 2006. Abnormal eggs and incubation behavior in Northern Bobwhite. Wilson Journal of Ornithology 118:114–116.

Koenig, W. D. 1980. The determination of runt eggs in birds. Wilson Bulletin 92:103–107.

Mallory, M. L., L. Kiff, R. G. Clark, T. Bowman, P. Blums, A. Mednis, and R. T. Alisauskas. 2004. The occurrence of runt eggs in waterfowl clutches. Journal of Field Ornithology 75:209–217.

Mulvihill, R. S. 1987. Runt eggs: a discovery, a synopsis, and a proposal for future study. North American Bird Bander 12:94–96.

Pearl, R. and M. R. Curtis. 1916. Studies on the physiology of reproduction in the domestic fowl—XV. Dwarf eggs. Journal of Agricultural Research 6:977–1042.

ROMANOFF, A. L. AND A. J. ROMANOFF. 1949. The avian egg. John Wiley and Sons, New York, USA.

ROTHSTEIN, S. I. 1973. The occurrence of unusually small eggs in three species of songbirds. Wilson Bulletin 85:340–342.

VANGILDER, L. D. 1992. Population dynamics. Pages 144–164 *in* The Wild Turkey: biology and management (J. G. Dickson, Editor). Stackpole Books, Harrisburg, Pennsylvania, USA.

WHITE, G. C. AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

The Wilson Journal of Ornithology 120(1):228–230, 2008

Barred Forest Falcon (*Micrastur ruficollis*) Predation on Relatively Large Prey

Fábio Röhe[1,3,4] and André Pinassi Antunes[2]

ABSTRACT.—We describe three successful predation events by the Barred Forest Falcon (*Micrastur ruficollis*) in the Atlantic Forest of coastal southeast Brazil. The prey items were a Plumbeous Pigeon (*Patagioenas plumbea*), a Brown Tinamou (*Crypturellus obsoletus*), and a large toad (*Chaunus ictericus*). This is the first report of successful attacks on prey heavier than the forest falcon, of which none was successfully carried away. These large prey items represent a tradeoff between high nutrient value and safety of carrying prey to a secure perch. *Received 16 November 2005. Accepted 23 July 2006.*

The Barred Forest Falcon (*Micrastur ruficollis*) is a small neotropical falconid weighing an average of 168 g for males and 233 g for females (Thorstrom 2000). It lives in dense primary or secondary forest where it is known to feed on a variety of small vertebrates and large invertebrates (Sick 1993). Studies of its diet are few (del Hoyo et al. 1994), the most detailed of which (405 prey identified) found reptiles to be the most important group, in terms of frequency, followed by birds. However, both were equal in biomass captured and delivered to nests during the breeding season (Thorstrom 2000). There is one example of predation on a hummingbird (Nunnery et al. 2002) and fruit consumption has been reported (Thorstrom 1996). Hilty and Brown (1986) reported the forest falcon is believed to specialize mostly on small birds, but are not specialists on them (Thorstrom 2000).

Forest falcons are regularly captured in Amazonian forest mist nets attacking small birds already caught in the nets (Mario Cohn-Haft, pers. comm.). They also follow swarms of army ants at times, presumably hunting either fleeing insects or other birds that follow the ants (Willis et al. 1983). The largest prey described weighed 160 g, roughly the minimum weight of the predator (Thorstrom 2000). We describe three cases in the Brazilian Atlantic rainforest of *M. ruficollis* successfully taking prey larger than itself, and briefly discuss the implications for the foraging and breeding ecology of the species. The bird prey weights were obtained from Sick (1993, 1997).

OBSERVATIONS

All of our observations were by chance, during the day, in the course of other research in the Brazilian State of São Paulo. The three sightings possibly involve three different individuals, based on the distances between sites of at least 3 km. The three observations were on dirt roads among patches of eucalyptus (*Eucalyptus saligna*) plantations and Atlantic forest on private farms (23° 55′ S, 47° 41′ W)

[1] Coordenação de Pesquisas em Ecologia (CPEC), INPA—Instituto Nacional de Pesquisas da Amazônia.

[2] Laboratório de Herpetologia, Departamento de Zoologia, Universidade Estadual Paulista—UNESP, Rio Claro, São Paulo, Brazil.

[3] Current address: WCS—Wildlife Conservation Society, Av. General Rodrigo Octávio Jordão Ramos, 3000, Japiim. Instituto de Ciências Biológicas, Departamento de Biologia. Bloco Projecto Sauim-de-Coleira/WCS.

[4] Corresponding author; e-mail: fabiorohe@gmail.com

at an altitude of 650–980 m in the Serra do Mar coastal mountain range.

We observed a forest falcon in May 2001 on the ground eating a Plumbeous Pigeon (*Patagioenas plumbea*), the breast of which was already mostly consumed. The falcon flushed on our approach trying unsuccessfully to carry the prey, which it dropped after dragging it for 1 m. This pigeon has an average weight of 231 g. We observed another forest falcon in January 2002 on the ground eating a large toad (*Chaunus ictericus*). Adult males of this toad species, approximately the size we observed, weigh 200–250 g (A. P. Antunes, pers. obs.). The raptor was eating from the throat region, possibly avoiding the area of the paratoid glands.

In August 2003 we encountered a falcon on the ground stripping the neck feathers from a live Brown Tinamou (*Crypturellus obsoletus*; weight 480 g). The forest falcon was grasping the tinamou's dorsum and flapping the wings slightly. The prey showed no external evidence of injury but, after the forest falcon released it, the tinamou remained on its back, apparently unable to move. The raptor flushed upon our arrival trying to carry the prey, which it was unable to move.

One additional observation occurred at approximately sea level at Itamambuca Beach, Ubatuba Municipality, in October 2003. A Barred Forest Falcon landed on a perch 1 m above the ground and 1.5 m from a large terrestrial Black-white Tegu (*Tupinambis merianae*), which we had been observing. This lizard was ~1 m in length (including tail) and weighed ~1.0–1.5 kg (A. P. Antunes, pers. obs.). The hawk watched the lizard closely and flushed after noticing our presence.

DISCUSSION

The possibility of vehicle strikes was discarded in the predation events because: (1) the Plumbeous Pigeon predation site can not be accessed by car, (2) only our vehicle was allowed on the farm in the case of the tinamou, and (3) no signs of flattening of the toad were observed.

Other reports of toad predation by hawks have included a White-tailed Hawk (*Buteo albicaudatus*) eating just the legs of *Chaunus marinus* (Sick 1997) and a Red-tailed Hawk (*B. jamaicensis*) preying on *Anaxyrus boreas* (Jones and Stiles 2000).

Our observations describe predation by Barred Forest Falcons on two different animal classes (birds and amphibians), reinforcing the importance of these groups in its diet. This is the first report of successful attacks by *M. ruficollis* on prey heavier than 160 g. Thorstrom (2000) documented maximum weight of prey based on estimated weight of items taken and delivered to nests by breeding forest falcons. Prey items must be sufficiently light for the adult to carry in flight. We documented captured prey as much as twice the weight of a Barred Forest Falcon. None of these larger prey items could be carried by the forest falcon suggesting the threshold weight for carrying is roughly that of the falcon. Thorstrom (2000) reported the Collared Forest Falcon (*Micrastur semitorquatus*) (average body mass for females = 869 g) captured an Ocellated Turkey (*Meleagris ocellata*) weighing 3 kg which represented ~3.5 times the body mass of the female forest falcon. This female fed and stayed near this kill for several days, and later carried pieces of the carcass to the nest where she was attending two nearly-fledged nestlings (Russell Thorstrom, pers. comm.).

These observations suggest that predation on considerably larger prey may not be uncommon when forest falcons are not associated with nesting, when pieces of the carcass are carried to the nest. The risk of preying on animals that must be consumed *in situ* may be compensated by the obviously greater nutrient value these prey represent.

ACKNOWLEDGMENTS

We thank Mario Cohn-Haft and T. M. Sanaiotti for valuable comments and help with revision of the manuscript. We thank J. A. Sedgwick, R. O. Bierregaard, C. M. White, and Russell Thorstrom for review and suggestions that improved this paper. We thank Eucatex S/A for logistic support and authorization to develop research projects in its area, and FAPESP (Processos #01/13341-3 and #04/10974-3) for financial support.

LITERATURE CITED

DEL HOYO, J., A. ELIOT, AND J. SARAGATAL. 1994. Handbook of the birds of the world. Volume 2. New world vultures and guineafowl. Lynx Ediciones, Barcelona, Spain.

HILTY, S. L. AND W. L. BROWN. 1986. A guide to the

birds of Colombia. Princeton University Press, Princeton, New Jersey, USA.

Jones, M. S. and B. Stiles. 2000. *Bufo boreas* (Boreal Toad). Predation. Herpetological Review 31:99.

Nunnery, T., L. Linda, and M. R. Welford. 2002. Barred Forest-falcon (*Micrastur ruficollis*) predation on a hummingbird. Journal of Raptor Research 36:239–240.

Sick, H. 1993. Birds in Brazil—a natural history. Princeton University Press, Princeton, New Jersey, USA.

Sick, H. 1997. Ornitologia Brasileira. Nova Fronteira. Rio de Janeiro, Brazil.

Thorstrom, R. 1996. Fruit-eating behavior of a Barred Forest-falcon. Journal of Raptor Research 30:44.

Thorstrom, R. 2000. The food habits of sympatric forest-falcons during the breeding season in northeastern Guatemala. Journal of Raptor Research 34:196–202.

Willis, E. O., D. Wechsler, and F. G. Stiles. 1983. Forest-falcons, hawks, and a pygmy-owl as ant followers. Revista Brasileira de Biologia 43:23–28.

The Wilson Journal of Ornithology 120(1):231–237, 2008

Ornithological Literature

Compiled by Mary Gustafson

GEORGE MIKSCH SUTTON: ARTIST, SCIENTIST, AND TEACHER. By Jerome A. Jackson. University of Oklahoma Press, Norman, USA. 2007: 239 pages, 29 figs., and 27 color plates. ISBN: 978-0-8061-3745-2. $29.95 (cloth).—Sutton was one of the premier bird illustrators and artists of the 20th century, and a major figure in North American ornithology. This book is a definitive biography of Sutton and nicely complements Sutton's autobiographical travelogues and autobiography of his early years (*Bird Student*, 1980, University of Texas Press, Austin). This story of the life and work of George Miksch Sutton draws upon Jackson's numerous personal recollections of Sutton as well as in-depth interviews with dozens of Sutton's contemporaries, colleagues, family, and friends (65 are listed in the Acknowledgments). It also draws upon the voluminous Sutton correspondence archived at the Universities of Oklahoma, Michigan, and Cornell, and the Smithsonian Archives in Washington, D.C.

The book follows an essentially chronological format. The first chapter, "Family Ties," traces Sutton's ancestry back through two generations and emphasizes the closeness of the Sutton family as well as Sutton's early interest in birds. The next three chapters trace in more detail Sutton's growth and development as an artist, ornithologist, and person, from his birth in rural Bethany, Nebraska (Sutton's father was 'Professor of Eloquence' at Cottner College in Bethany, Nebraska), his early encounters with birds, mail-order taxidermy lessons, and the family's move to Bethany, West Virginia. We read of the publication of Sutton's first articles in *Bird-Lore*, and his mentoring by Louis Agassiz Fuertes, to his entry into professional ornithology through working with W. Clyde Todd at the Carnegie Museum in Pittsburgh. Sutton's interest in birds and art date back to his early years (he was selling bird drawings for a penny or so each by age seven). Chapters follow on Sutton's role as Pennsylvania State Ornithologist, his expedition to Southampton Island in the Canadian Arctic, his doctoral work at Cornell University under the mentorship of Arthur A. Allen, his activities in the army during World War II, and his growing love of the Arctic, the Neotropics, and the southwestern United States that was to play a major role in his art and science. The chapter "The Michigan Years," traces Sutton's long relationship with Josselyn Van Tyne that included collaboration on research and the Wilson Ornithological Club (now Society) that led to Sutton's full-time employment at the University of Michigan. Sutton's complex relationship with Cornell University did not endure and he was pleased to move to the greener pastures of the University of Michigan. His relationship with Van Tyne, however, quickly deteriorated, and this led, in 1952, to a shift to the University of Oklahoma, where Sutton would spend the final 30 years of his life. A chapter entitled "Teacher, Conservationist, Philanthropist," emphasizes these aspects of Sutton's professional life. "From Illustration to Fine Art" traces Sutton's struggles and triumphs with bird illustration and bird art. The concluding chapter, "Ovenbird and Golden Eagle," follow Sutton in his last days and includes Sutton poetry, demonstrating yet another facet of Sutton's personality and accomplishments. An Appendix lists the many graduate students that Sutton mentored. A 26-page section of end notes documents the scholarly research that Jackson did for this portrait of George Miksch Sutton. A section, "Works by George Miksch Sutton," presents an exhaustive bibliography of Sutton's published works that runs to more than 450 entries, and includes nearly a dozen books beginning in 1928 with *An Introduction to the Birds of Pennsylvania* (J. Horace, Harrisburg), followed in 1934 by *Eskimo Year* (McMillan, New York) and ending with the posthumous *Birds Worth Watching* (1986, University of Oklahoma Press, Norman). A final section, "Works Illustrated by George Miksch Sutton," lists 40 books and

monographs written by other authors but illustrated in part or entirely by Sutton. He, of course, illustrated many of his own written works.

Jackson has captured Sutton's personality in words, and the 27 color plates and more than a dozen line drawings illustrate Sutton's growth as an artist and illustrator, and demonstrate the diversity of his artwork. This thoroughly researched and well-written book is a significant contribution to both the history of ornithology and the history of bird illustration and art.—WILLIAM E. DAVIS JR., Professor Emeritus, Boston University, 23 Knollwood Drive, East Falmouth, MA 02536, USA; e-mail: wedavis@bu.edu

IVORYBILL HUNTERS: THE SEARCH FOR PROOF IN A FLOODED WILDERNESS. By Geoffrey E. Hill. Oxford University Press, New York, USA. 2007: 260 pages, 74 black and white photographs, 4 maps, and 1 diagram. ISBN: 978-0-19-532346-7. $24.95 (cloth).—This is another in a series of books that have recently appeared about the Ivory-billed Woodpecker (*Campephilus principalis*) (e.g., T. Gallagher, 2005, *The Grail Bird: Hot on the Trail of the Ivory-billed Woodpecker*, Houghton Mifflin, Boston, MA, USA; J. Jackson, 2006, *In Search of the Ivory-billed Woodpecker*, Smithsonian Books, Washington, D.C., USA). Long thought by many to be extinct in the United States (the last fully documented sighting of ivorybills was in the 1930s), recent reports of sightings have rekindled interest and hope that this largest of the North American woodpeckers may still be extant. In this book Hill recounts a search for ivorybills in northwest Florida and reports in an Appendix on 15 "... Observations of Ivory-billed Woodpeckers" and 43 "... sound detections of Ivory-billed Woodpeckers" made between May 2005 to May 2006. Unfortunately, no photographic evidence was gathered that would offer irrefutable proof that the ivorybill was the species that was seen and heard. The book is primarily a tale of the search for ivorybills. As the author explains in the Preface: "I focus primarily on the search and the searchers rather than the woodpecker. After all, the search for and rediscovery of the Ivory-billed Woodpecker is a human tale. The ivorybills of the Choctawhatchee River Wetlands in the panhandle of northern Florida eat their grubs, cut their cavities, and raise their young as they have always done." Hill also emphasizes in the Preface that: "This book is story, not a technical report" and contains neither footnotes nor in-text citations. It does, however, craft arguments directed at convincing the reader that the ivorybills he reports on are real.

After an introductory chapter that shares some 20th century ivorybill history, the second chapter: "A Most Improbable Discovery," recounts the decision to kayak the Choctawhatchee River: "No trip could have been conceived more whimsically," (page 20) and the unexpected hearing of "Loud knocking," and sighting of a bird that could have been an ivorybill: "it was big and mostly black with a lot of white flashing on the top and bottom of the back of its wings" (page 23) was remarkable. The third chapter: "From Possible to Virtual Certainty," recounts the adventures of Hill and several of his graduate students in subsequent trips, this time sightings included two birds by one field assistant, and Hill was convinced there were really ivorybills there. Chapters follow on planning for a systematic search for the ivorybills, securing of limited funding for the project, the habitat and logging history of the Choctawhatchee River lands, and a series of adventures and misadventures by Hill and his associates as they searched for Ivory-billed Woodpeckers. In a chapter: "Good Science, Bad Science, or No Science At All" the author emphasizes that searching for Ivorybills is not science, and explores the controversy around recent reported sightings and adds some historical perspective. Another chapter highlights the searches made for tangible evidence that included systematic searches for possible nest or roosting sites, feeding marks on trees, video and audio recordings, and presents the results as a circumstantial case for the existence of ivorybills through spectrograms of "double knocks" and "kent calls" recorded during searches. It is abundantly clear the author is convinced that ivorybills are alive and well in his study area: "By June 2005, Tyler, Brian, and I knew that there was at least one ivorybill near the mouth of Bruce Creek in the Choctawhatchee

River bottom" (page 143), and in the Epilogue: "The discovery of a population of ivorybills along the Choctawhatchee River in Florida is an exciting and fun birding event." This book makes a case for this reality. However, to date (including the 2007 field season) no irrefutable photographic evidence has been produced. An interesting parallel exists between the ivorybills and the Tasmanian Tiger (*Thylacinus cyanocephalus*), a marsupial carnivore. The last tiger in captivity died in 1936, but sightings have been reported ever since, some by qualified biologists. However, no road-killed tigers have been found nor has indisputable photographic evidence been produced. In the absence of irrefutable evidence, and with the intrinsic problems faced by rare animals, much of the scientific community is likely to remain skeptical of the continued existence of either Ivory-billed Woodpeckers or Tasmanian Tigers.

Hill's book is written for a popular audience and is not a scientific work. In any event, it chronicles an interesting adventure story, and I recommend it as a good read.—WILLIAM E. DAVIS JR., Professor Emeritus, Boston University, 23 Knollwood Drive, East Falmouth, MA 02536, USA; e-mail: wedavis@bu.edu

HANDBOOK OF AVIAN HYBRIDS OF THE WORLD. By Eugene M. McCarthy. Oxford University Press, New York, USA. 2006: 583 pages and 20 figures. ISBN: 0-19-518323-1. $89.50 (cloth).—Research on avian hybridization played a key role in the development of the New Synthesis (Mayr 1942), and remains at the forefront of modern evolutionary biology (Prager and Wilson 1975, Grant and Grant 1992, Price 2008). Given the importance of hybridization in evolutionary biology, taxonomy, conservation biology, behavioral ecology, and avicultural and poultry science, it is surprising that the last English language compilation of avian hybrids was published nearly a half century ago (Gray 1958). *Handbook of Avian Hybrids of the World* fills this vacuum with an exhaustive listing of natural hybrids and those obtained in aviaries or through breeding experiments. McCarthy's intent (Preface) to "provide basic information about each of the thousands of types of reported avian crosses, to provide access to documenting literature, and to familiarize readers with the nature of avian hybridization," succeeds in most respects.

The book is organized in five main sections: introduction (35 pages), hybrid accounts (299 pages), appendices (15 pages), literature cited (160 pages), and index of English and scientific names (69 pages). The introduction outlines the organizational scheme of hybrid accounts, briefly addresses hybrid fertility, taxonomy, identification of hybrids, expression of hybrid traits, hybrid zones, and causes of hybridization. McCarthy's review of each of these topics is brief, but the sections that address the hybrid diagnosis, the process by which parental species may be ascertained from morphology (Graves 1990), are too general to be of much use. The reader is left with no real idea of the systematic processes that are required to accurately assign the parentage of a hybrid or how alternative hypotheses may be rejected. McCarthy makes a number of poorly supported claims in the introduction—for example, that heterosis or hybrid luxuriance (when the measurements of hybrids fall outside the cumulative range of measurements observed in the parental species) has been observed in avian hybrids. To my knowledge, there are no well-documented cases of hybrid luxuriance in birds. References that purport such a phenomenon insufficiently sampled the range of morphological variation in the parental species.

Hybrid accounts and the cited literature form the core of the book. A typical hybrid account takes the form:

> *Selasphorus ardens* (Glow-throated Hummingbird)
> × *Selasphorus scintilla* (Scintillant Hummingbird) NHR. BRO. Panama. Panov 1989; Stiles 1983.

McCarthy introduces a coding system that permits the reader to quickly note whether hybridization occurs under natural conditions or in captivity, the fertility of hybrids, cross reversibility, breeding range overlap, etc. This is a significant organizational advance over past compilations of hybrid literature (Gray 1958, Panov 1989). Interesting and useful annotations accompany many of the hybrid

crosses, although a small fraction of the accounts I checked garbled the facts or presented erroneous information (e.g., Bogotá Sunangel, *Heliangelus zusii*; Graves 1993]). The appendix listing aviary hybrids of canaries is particularly fascinating because it amply demonstrates how slowly genetic barriers to hybridization evolve among oscines.

Powerful internet search engines make the task of searching the hybrid literature far easier than it was just a decade ago. Nevertheless, McCarthy's compilation of the literature is impressive. His quest for published and unpublished hybrid records probed the nooks and crannies of internet web sites, birding journals, birder's trip lists, museum data bases, and the largely inaccessible 19th and early 20th century avicultural and ornithological literature housed only in a few museum and university libraries. However, those who cast a wide net had better be prepared to throw back the by-catch. Unfortunately, McCarthy kept it all—the good, the bad, and the vague. The lack of discrimination reduces the usefulness of his work because readers will have to dig deeply into the cited works to evaluate the quality of the documentation. As an example of material that should have been rejected, a simple entry ("Magpie Robin × White-rump Shama; Pai, Thailand") in a birder's trip log posted on an internet web site (Appendix 3, ASIA96) constituted the sole authority for the hybrid cross, *Copsychus malabaricus* × *C. saularis*. Regrettably, considerable numbers of insufficiently documented hybrids extracted from internet sources and print literature were included. Curiously, McCarthy also included records of *inferred* hybridization where no hybrid offspring are known to exist. To his credit, McCarthy attempted to break the chain of citation for some hybrid crosses that have been erroneously reported in the literature, but he also propagated several hybrid records (e.g., *Selasphorus ardens* × *S. scintilla*) created by Panov (1989) and managed to invent new ones on his own (e.g., White-bearded Manakin [*Manacus manacus*] × Crimson-hooded Manakin [*Pipra aureola*]).

"Double entry" is another persistent problem in the hybrid accounts. This occurs when two or more parental hypotheses have been proposed for an enigmatic specimen leading to the listing of two hybrid combinations. Considerable background research is often necessary to detect "double entry" errors. Spelling errors are few and far between (e.g., "*Metallura altricularis*"). However, there seemed to be an unusual number of citations assigned inappropriately to hybrid records. In all fairness, keeping track of 5,000+ cited sources and thousands of reported hybrids is no mean feat. Still, a pre-publication appraisal by reviewers familiar with the avian hybrid literature may have eliminated many of the factual errors in the book.

The damage caused by indiscriminate publication of insufficiently or incompetently diagnosed hybrids is threefold. First, it introduces unsupported records into the literature that are maddeningly difficult to eradicate once published. Despite the caveats mentioned in McCarthy's introduction, less savvy users may naturally assume the documentation backing hybrid records in the book meets some quality threshold. Unfortunately, the quality of hybrid records runs the gamut from wild guesses and unadorned assertions posted on internet web sites to detailed diagnoses published in reputable peer-reviewed journals (Banks and Johnson 1961, Graves 1996). Lastly, inclusion of hybrids based on sight records and photographs of free-living birds endorses the notion promoted in many birding publications that accurate diagnosis of hybrids observed in the field is not only possible but probable. While some hybrids may certainly be identified under field conditions (e.g., *Vermivora chrysoptera* [Golden-winged Warbler] × *V. pinus* [Blue-winged Warbler]), an accurate hybrid diagnosis in most taxonomic groups, particularly those with drab plumages (e.g., *Empidonax*, *Contopus*, *Phylloscopus*) or from regions of high species diversity, can seldom be accomplished under field conditions or from photographs of free-living birds. Detailed hybrid diagnoses based on fully vouchered specimens (available for repeated morphological and genetic analyses) remain the gold standard in the field (Hennache et al. 2003). Whenever possible, hybrid birds (particularly rare or possibly unknown combinations) should be collected for scientific study. The scientific value of such specimens is significant as demonstrated by the voluminous literature on avian hybridization. Every banding station should possess a scientific collect-

ing permit that allows hybrid birds to be collected for scientific study. Museums are more than willing to process and archive such specimens for use by the greater scientific community. McCarthy lists museum specimen numbers in the annotations for some hybrid records. Although it would entail a Herculean effort, the value of future editions of this book would be greatly enhanced if the availability of voucher specimens and relative quality of documentation were noted for all hybrid combinations.

The most serious problem with compilations of this nature is that synthesists may be tempted to use the data for phylogenetic or macroecological studies of hybridization. In many research programs, it is standard practice to assign students the task of converting catalogs of this type into spreadsheet data files for analyses by senior investigators. However, few senior investigators will have the time or library resources to examine the original citations or the expertise and comparative material needed to vet supposed cases of hybridization. This would be difficult to do outside a large museum. Macroecological and phylogenetic analyses based on unexpurgated data extracted from hybrid catalogs constitute poor science, *user caveo.*

Who needs this book? Every museum and university library needs a copy of *Handbook of Avian Hybrids of the World.* I will use it frequently as a convenient and comprehensive guide to the hybrid literature. Aviculturists may also find the contents useful but I suspect the vast majority of birders would not use it enough to warrant its purchase.—GARY R. GRAVES, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013, USA; e-mail: gravesg@si.edu

LITERATURE CITED

Banks, R. C. and N. K. Johnson. 1961. A review of North American hybrid hummingbirds. Condor 63:3–28.

Grant, P. R. and B. R. Grant. 1992. Hybridization of bird species. Science 256:193–197.

Graves, G. R. 1990. Systematics of the "Green-throated Sunangels" (Aves: Trochilidae): valid taxa or hybrids? Proceedings of the Biological Society of Washington 103:6–25.

Graves, G. R. 1993. Relic of a lost world: a new species of sunangel (Trochilidae: *Heliangelus*) from "Bogota". Auk 110:1–8.

Graves, G. R. 1996. Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes. Proceedings of the Biological Society of Washington 109:373–390.

Gray, A. P. 1958. Bird hybrids. Commonwealth Agricultural Bureaux, Bucks, England.

Hennache, A., P. Rasmussen, V. Lucchini, S. Rimondi, and E. Randi. 2003. Hybrid origin of the Imperial Pheasant *Lophura imperialis* (Delacour and Jabouille, 1924) demonstrated by morphology, hybrid experiments, and DNA analyses. Biological Journal of the Linnean Society 80:573–600.

Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York, USA.

Panov, E. N. 1989. Natural hybridisation and ethological isolation in birds (in Russian). Nauka, Moscow, USSR.

Prager, E. M. and A. C. Wilson. 1975. Slow evolutionary loss of the potential for interspecific hybridization in birds: a manifestation of low regulatory evolution. Proceedings of the National Academy of Sciences USA 72:200–204.

Price, T. 2008. Speciation in birds. Roberts and Company, Greenwood Village, Colorado, USA.

Stiles, F. G. 1983. Systematics of the southern species of *Selasphorus* (Trochilidae). Auk 100:311–325.

HANDBOOK OF THE BIRDS OF THE WORLD, VOLUME 11: OLD WORLD FLYCATCHERS TO OLD WORLD WARBLERS. Edited by Josep del Hoyo, Andrew Elliott, and David Christie. Lynx Edicions, Barcelona, Spain. 2006: 798 pages, 55 color plates, more than 300 photographs, and 723 maps. ISBN: 84-96553-06-X. $250.00 (cloth).—*Handbook of the Birds of the World* continues with Volume 11 in the landmark series. This volume contains seven Families of Passerines including Old World Flycatchers, Batises and Wattle-eyes, Fantails, Monarch-flycatchers, Kinglets and Firecrests, Gnatcatchers, Cisticolas and Allies, and Old World Warblers. Each Family account has sections outlining familial characteristics including systematics, morphology, habitat, habits, voice, food and feeding, breeding, movements, relationship with man, status and conservation, and a general bibliography. This section is lavishly illustrated with exquisite photographs that capture the birds in intimate moments bathing, roosting, nesting, caring for young, feeding, or just being birds.

The species accounts start with a color plate

followed by individual accounts for the species on the plate. The plates are up to the excellent standards of the series with accurate shapes and well reproduced colors. The text for each species includes the scientific name as well as the name in English, French, German, Spanish, and other common names. Many of the same subjects in the family account are addressed for each species individually; other topics include subspecies and distribution, descriptive notes, and a range map.

The editors went to great lengths to ensure this volume was up to date at the time it went to press. The book includes two species first described in 2006, the Dark Batis (*Batis crypta*) and the Odedi Bush-warbler (*Cetti haddeni*). Also included is a photograph in hand of the Large-billed Leaf Warbler (*Acrocephalus orinus*) trapped in March 2006, the first record since the species was discovered in 1867; remarkable for a book with a publication date of 2006. The volume is well-edited. I found one minor formatting fault and one apparent miscount.

The series includes a Foreword to each volume on some aspect of ornithology. This volume has a Foreword by Çağan Şekercioğlu titled *The Ecological Significance of Bird Populations.* This paper describes the ecological processes that birds undertake (pollination, seed dispersal, predation, carrion consumption, etc.) and the effect that declines in bird populations have on the ecosystem if those processes are lost. This is a thought-provoking article, although I would have preferred having the references with the article rather than mixed with the general references for the entire volume.

I highly recommend this series.—MARY GUSTAFSON, Rio Grande Joint Venture, Texas Parks and Wildlife Department, 2800 South Bentsen Palm Drive, Mission, TX 78572, USA; e-mail: mary.gustafson@tpwd.state.tx.us.

TEXAS QUAILS: ECOLOGY AND MANAGEMENT. Edited by Leonard A. Brennan. Texas A&M University Press, College Station, USA. 2007: ix + 491 pages, with black and white photographs, tables, graphs, and maps. ISBN-13: 978-1-58544-503-5, $40.00 (cloth).—This hefty, hardback volume addresses four quail species that inhabit the state of Texas; Gambel's Quail (*Callipepla gambelii*), Montezuma or Mearns' Quail (*Cytonyx montezumae*), Northern Bobwhite (*Colinus virginianus*), and Scaled Quail (*Callipepla squamata*).

This book is a collection of essays and papers divided into three sections. One section deals with the life history of the four native quail species occurring in Texas. Another section addresses the birds' populations in each of the eco-regions as well as acknowledging the challenges of research; past, present, and future. In addition, this section addresses management opportunities for these species in their particular eco-region. A third section attends to the rich cultural heritage of quail and quail hunting in the Lone Star State, as well as the future of these birds in Texas.

Within each of these three sections are chapters written by some of the best quail researchers in Texas and Oklahoma. Overall, the chapters are written well, enhanced by relevant black and white photographs. Tables and graphs often appear on the same or adjacent page which aids in further illustrating the discussion and/or research. Quotations and documentation are cited at the end of the sentence by author(s) and year in parentheses. Of particular note is the extensive bibliography section toward the back of the book, labeled "References." For the researcher, the book represents an invaluable source on the history, ecology, management practices, and guidelines for the present and future. It also provides an appreciable inventory of past works.

As valuable as this volume is for the researcher, it is not exclusively intended for the professional ornithologist. The book has a number of chapters that address issues applicable to wildlife managers and landowners. Chapters describing past methodologies (successful or failed), and recommendations regarding future practices are present in abundance. Many of the recommendations are born of mistakes, misunderstanding, and errors from the past. Much of existing research, in particular regarding Scaled, Gambel's and Montezuma Quail is from other states, most notably Arizona, New Mexico, and western Oklahoma. This collection will be of interest to ecologists, conservationists, citizen-scien-

tists, and anyone with interest in quail and wildlife conservation. Despite the title, this book's value is not limited to Texas but the wider southwestern United States. Managing for suitable native habitat for quail species is quite often in concert with restoring habitat for "non-game" species as well.

This is an impressive comprehensive, up-to-date collection of Texas and Southwest research reports detailing quail behavior, life history, ecology, management, native habitat, and its restoration. It will be of interest to those concerned about the fragmentation and loss of wild spaces. This book will help inform those concerned with the survival, not just of any one particular species, but of the cultural, historical, and aesthetic sensitivity of humans.

This book would be a significant reference addition to the library of anyone interested in wildlife. I recommend it.—MATTHEW W. YORK, 9910 Ramblewood Drive, Waco, TX 76712, USA; e-mail: mwy391@yahoo.com

Editor's Comments

Production of Volume 119 (2007) went relatively smoothly thanks to reviewers, authors, and the staff at Allen Press. We are receiving and publishing more manuscripts, and expect this trend to continue. We are also receiving more manuscripts from outside of North America, especially from Central and South America. We also expect this trend to continue. Publishing manuscripts from across the world has some pitfalls as usage of common and scientific names is frequently not consistent. Effective 1 January 2008, we now follow Gill and Wright (Gill, F. and M. Wright, 2006. Birds of the world. Recommended English names. Princeton University Press, Princeton, New Jersey, USA and Oxford, United Kingdom.) for all non-North American species. This reference source was published on behalf of the International Ornithological Congress. We will listen to rational views on changes in nomenclature (especially newly described species) as they become published. We continue to follow the American Ornithologists' Union for North American species except for some species that are not primarily residents or migrants in North America.

We believe we have outstanding papers in this issue and more are scheduled for later issues in Volume 120. We continue to seek reviewers capable of providing timely and thorough reviews of manuscripts. Please help us access current e-mail addresses via updating The Flock or direct communication with our office.

Clait E. Braun
Editor, 2008

THE WILSON JOURNAL OF ORNITHOLOGY

Editor CLAIT E. BRAUN
5572 North Ventana Vista Road
Tucson, AZ 85750-7204
E-mail: TWILSONJO@comcast.net

Editorial Assistant NANCY J. K. BRAUN

Editorial Board RICHARD C. BANKS
KATHY G. BEAL
JACK CLINTON EITNIEAR
SARA J. OYLER-McCANCE

Review Editor MARY GUSTAFSON
Texas Parks and Wildlife Department
2800 South Bentsen Palm Drive
Mission, TX 78572, USA
E-mail: WilsonBookReview@aolcom

GUIDELINES FOR AUTHORS

Please consult the detailed "Guidelines for Authors" found on the Wilson Ornithological Society Web site (http://www.ummz.umich.edu/birds/wos/index.html). All manuscript submissions and revisions should be sent to Clait E. Braun, Editor, *The Wilson Journal of Ornithology*, 5572 North Ventana Vista Road, Tucson, AZ 85750-7204, USA. *The Wilson Journal of Ornithology* office and fax telephone number are (520) 529-0365. The e-mail address is TWilsonJO@comcast.net.

NOTICE OF CHANGE OF ADDRESS

Notify the Society immediately if your address changes. Send your complete new address to Ornithological Societies of North America, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

The permanent mailing address of the Wilson Ornithological Society is: %The Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109. Persons having business with any of the officers may address them at their various addresses given on the inside of the front cover, and all matters pertaining to the journal should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Timothy J. O'Connell, Department of Natural Resource Ecology and Management, Oklahoma State University, 205 Life Sciences West, Stillwater, OK 74078; e-mail: oconnet@okstate.edu

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution. The fund will be administered by the Library Committee. Robert Payne, University of Michigan, is Chairman of the Committee. The Library currently receives over 200 periodicals as gifts and in exchange for *The Wilson Journal of Ornithology*. For information on the Library and our holdings, see the Society's web page at http://www.ummz.umich.edu/birds/wos/index.html. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: Josselyn Van Tyne Memorial Library, Museum of Zoology, The University of Michigan, 1109 Geddes Avenue, Ann Arbor, MI 48109-1079, USA. Contributions to the New Book Fund should be sent to the Treasurer.

This issue of *The Wilson Journal of Ornithology* was published on 12 March 2008.

Continued from outside back cover

159 Timing and location of mortality of fledgling, subadult, and adult California Gulls
Bruce H. Pugesek and Kenneth L. Diem

167 Effects of predation and food provisioning on Black Tern chick survival
Shane R. Heath and Frederick A. Servello

176 Use of clay licks by Maroon-fronted Parrots (*Rhynchopsitta terrisi*) in northern Mexico
Rene A. Valdés-Peña, Sonia Gabriela Ortiz-Maciel, Simon O. Valdez Juarez, Ernesto C. Enkerlin Hoeflich, and Noel F. R. Snyder

181 Cavity number and use by other species as correlates of group size in Red-cockaded Woodpeckers
John J. Kappes Jr.

Short Communications

190 First description of nests and eggs of two Hispaniolan endemic species: Western Chat-tanager (*Calyptophilus tertius*) and Hispaniolan Highland-tanager (*Xenoligea montana*)
Christopher C. Rimmer, Lance G. Woolaver, Rina K. Nichols, Eladio M. Fernández, Steven C. Latta, and Esteban Garrido

195 Foraging and nesting of the ʻAkikiki or Kauaʻi Creeper (*Oreomystis bairdi*)
Eric A. VanderWerf and Pauline K. Roberts

200 First observation of duetting in the Olive-backed Euphonia (*Euphonia gouldi*)
Thor Hanson

201 The display of a Reddish Hermit (*Phaethornis ruber*) in a lowland rainforest, Bolivia
Adam Felton, Annika M. Felton, and David B. Lindenmayer

205 Home range and habitat preferences of the Banded Ground-cuckoo (*Neomorphus radiolosus*)
Jordan Karubian and Luis Carrasco

209 Comparisons between juvenile and adult American Robins foraging for mulberry fruit
E. Natasha Vanderhoff and Perri K. Eason

214 Previously unknown food items in the diet of six neotropical bird species
Luis Sandoval, Esteban Biamonte, and Alejandro Solano-Ugalde

217 Anvil use by the Red-cockaded Woodpecker
Kristin J. Bondo, Lauren N. Gilson, and Reed Bowman

221 Gender identification of Grasshopper Sparrows comparing behavioral, morphological, and molecular techniques
Frank K. Ammer, Petra Bohall Wood, and Roger J. McPherson

226 Abnormal eggs of Rio Grande Wild Turkeys on the Edwards Plateau, Texas
Kyle B. Melton, Justin Z. Dreibelbis, Ray Aguirre, Bret A. Collier, T. Wayne Schwertner, Markus J. Peterson, and Nova J. Silvy

228 Barred Forest Falcon (*Micrastur ruficollis*) predation on relatively large prey
Fábio Röhe and André Pinassi Antunes

231 Ornithological Literature
Compiled by Mary Gustafson

237 Editor's Comments

The Wilson Journal of Ornithology

(formerly *The Wilson Bulletin*)

Volume 120, Number 1 CONTENTS March 2008

Major Articles

1 A new White-eye (*Zosterops*) from the Togian Islands, Sulawesi, Indonesia
Mochamad Indrawan, Pamela C. Rasmussen, and Sunarto

10 The White-eyed Foliage-gleaner (Furnariidae: *Automolus*) is two species
Kevin J. Zimmer

26 Recent advances in the behavioral ecology of tropical birds
Bridget J. M. Stutchbury and Eugene S. Morton

38 Distribution, behavior, and conservation status of the Rufous Twistwing (*Cnipodectes superrufus*)
Joseph A. Tobias, Daniel J. Lebbin, Alexandre Aleixo, Michael J. Andersen, Edson Guilherme, Peter A. Hosner, and Nathalie Seddon

50 Natural history and behavior of the Aldabra Rail (*Dryolimnas* [*cuvieri*] *aldabranus*)
Ross M. Wanless and Philip A. R. Hockey

62 Post-fledging movement and spatial habitat-use patterns of juvenile Swainson's Thrushes
Jennifer D. White and John Faaborg

74 Spring migratory stopover of Swainson's Thrush along the Pacific Coast of southwest Costa Rica
Scott Wilson, Keith A. Hobson, Douglas M. Collister, and Amy G. Wilson

85 Demography of Eastern Yellow Wagtails at Cape Romanzof, Alaska
Heather M. Renner and Brian J. McCaffery

92 Breeding ecology of the Narcissus Flycatcher in north China
Ning Wang, Yanyun Zhang, and Guangmei Zheng

99 Reproductive success of House Wrens in suburban and rural landscapes
Michael J. Newhouse, Peter P. Marra, and L. Scott Johnson

105 Habitat selection and reproductive success of Cerulean Warblers in Indiana
Kirk L. Roth and Kamal Islam

111 Nesting biology of grassland birds at Fort Campbell, Kentucky and Tennessee
James J. Giocomo, E. Daniel Moss, David A. Buehler, and William G. Minser

120 Factors affecting home range size and movements of post-fledging grassland birds
Kimberly M. Suedkamp Wells, Joshua J. Millspaugh, Mark R. Ryan, and Michael W. Hubbard

131 Ecological factors affecting response of Dark-eyed Juncos to prescribed burning
Jinelle H. Sperry, T. Luke George, and Steve Zack

139 Winter habitat use by Boreal Chickadee flocks in a managed forest
Adam Hadley and André Desrochers

146 Long-term effects of wastewater irrigation on habitat and a bird community in central Pennsylvania
Adam T. Rohnke and Richard H. Yahner

153 Long-term trends in breeding birds in an old-growth Adirondack forest and the surrounding region
Stacy A. McNulty, Sam Droege, and Raymond D. Masters

Continued on inside back cover

24

The Wilson Journal of Ornithology

Volume 120, Number 2, June 2008

MCZ
LIBRARY
MAY 19 2009
HARVARD
UNIVERSITY

Published by the
Wilson Ornithological Society

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED 3 DECEMBER 1888

Named after ALEXANDER WILSON, the first American ornithologist.

President—James D. Rising, Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada; e-mail: rising@zoo.utoronto.ca

First Vice-President—E. Dale Kennedy, Biology Department, Albion College, Albion, MI 49224, USA; e-mail: dkennedy@albion.edu

Second Vice-President—Robert C. Beason, USDA, Wildlife Services, 6100 Columbus Avenue, Sandusky, OH 44870, USA; e-mail: beason@netzero.com

Editor—Clait E. Braun, 5572 North Ventana Vista Road, Tucson, AZ 85750, USA; e-mail: TWILSONJO@comcast.net

Secretary—John A. Smallwood, Department of Biology and Molecular Biology, Montclair State University, Montclair, NJ 07043, USA; e-mail: smallwoodj@montclair.edu

Treasurer—Melinda M. Clark, 52684 Highland Drive, South Bend, IN 46635, USA; e-mail: MClark@tcservices.biz

Elected Council Members—Carla J. Dove, Greg H. Farley, and Mia R. Revels (terms expire 2009); Rebecca Holberton, Robert S. Mulvihill, and Timothy O'Connell (terms expire 2010); Jameson F. Chace, Sara R. Morris, and Margaret A. Voss (terms expire 2011).

Membership dues per calendar year are: Active, $21.00; Student, $15.00; Family, $25.00; Sustaining, $30.00; Life memberships, $1,000.00 (payable in four installments).

The Wilson Journal of Ornithology is sent to all members not in arrears for dues.

THE WILSON JOURNAL OF ORNITHOLOGY

(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

All articles and communications for publications should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, MI 48109, USA.

Subscriptions, changes of address, and claims for undelivered copies should be sent to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710, USA. Phone: (254) 399-9636; e-mail: business@osnabirds.org. Back issues or single copies are available for $12.00 each. Most back issues of the journal are available and may be ordered from OSNA. Special prices will be quoted for quantity orders. All issues of the journal published before 2000 are accessible on a free web site at the University of New Mexico library (http://elibrary.unm.edu/sora/). The site is fully searchable, and full-text reproductions of all papers (including illustrations) are available as either PDF or DjVu files.

© Copyright 2008 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, KS 66044, U.S.A.

COVER: Wilson's Storm Petrel (*Oceanites oceanicus*). Illustration by Don Radovich.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

MCZ
LIBRARY
MAY 19 2009
HARVARD
UNIVERSITY

FRONTISPIECE. Male Ruffed Grouse (*Bonasa umbellus*) on a display log amidst a dense thicket of aspen (*Populus tremuloides*) in north-central Minnesota. Ruffed Grouse exhibit cyclic population fluctuations over much of their range. These cycles have been thought to be caused by predation, particularly by Northern Goshawks (*Accipiter gentilis*). Zimmerman et al. (page 239) report that winter weather conditions explained more variation in spring grouse indices than goshawks, but were not a definitive explanation of cycles. Photograph by Gordon W. Gullion (with permission of the University of Minnesota). The authors dedicate this paper

The Wilson Journal *of Ornithology*

Published by the Wilson Ornithological Society

VOL. 120, NO. 2 June 2008 PAGES 239–432

The Wilson Journal of Ornithology 120(2):239–247, 2008

NEW INSIGHT TO OLD HYPOTHESES: RUFFED GROUSE POPULATION CYCLES

GUTHRIE S. ZIMMERMAN,[1,2] RICK R. HORTON,[3,4] DANIEL R. DESSECKER,[5] AND R. J. GUTIÉRREZ[1,6]

ABSTRACT.—We examined factors hypothesized to influence Ruffed Grouse (*Bonasa umbellus*) population cycles by evaluating 13 *a priori* models that represented correlations between spring counts of male Ruffed Grouse drumming displays and these factors. We used AIC_c to rank the relative ability of these models to fit the data and used variance components analysis to assess the amount of temporal process variation in Ruffed Grouse spring counts explained by the best model. A hypothesis representing an interaction between winter precipitation and winter temperature was the top-ranked model. This model indicated that increased precipitation during cold winters (soft snow cover for roosting) was correlated with higher grouse population indices, but that increased precipitation during warm winters (snow crust effect) was correlated with lower spring counts. The highest ranked model (AIC_c weight = 0.45), explained only 17% of the temporal process variation. The number of migrating Northern Goshawks (*Accipiter gentilis*), which has been correlated with grouse cycles in previous studies, does not adequately explain, by itself, the variation in annual population indices of Ruffed Grouse. Other factors not considered in our analysis, such as endogenous mechanisms, parasites, or interactions among factors may also be important, which suggest that mechanisms mediating the Ruffed Grouse cycle still require investigation. *Received 17 March 2007. Accepted 17 August 2007.*

The Ruffed Grouse (*Bonasa umbellus*) is a widespread and important game bird in North America (Rusch et al. 2000). Population size of grouse is known to fluctuate through time and, in some areas, these fluctuations follow a cycle of ~10 years (Keith 1963, Rusch et al. 2000). Their population fluctuations and cycles have been studied extensively (Bump et al. 1947, Keith 1963, Gullion and Marshall 1968, Keith and Rusch 1989, Small et al. 1991). These studies have generated many hypotheses about mechanism(s) responsible for grouse cycles. Ideas advanced as mechanisms controlling grouse fluctuations range from the bizarre (e.g., rabbit [Lagomorpha] seasons were too long; Bump et al. [1947]) to the plausible (e.g., predation; Rusch et al. 2000). Most recently, some researchers have presented correlative data that suggest predation by

[1] Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, St. Paul, MN 55108, USA.

[2] Current address: U.S. Fish and Wildlife Service, Division of Migratory Bird Management, 11510 American Holly Drive, Laurel, MD 20708, USA.

[3] Ruffed Grouse Society, P. O. Box 657, Grand Rapids, MN 55744, USA.

[4] Current address: Minnesota Department of Natural Resources, Grand Rapids, MN 55744, USA.

[5] Ruffed Grouse Society, P. O. Box 2, Rice Lake, WI 54868, USA.

[6] Corresponding author; e-mail: gutie012@umn.edu

Northern Goshawks (*Accipiter gentilis*) and Great Horned Owls (*Bubo virginianus*) are most likely causing cyclic population fluctuations in Ruffed Grouse (Keith and Rusch 1989, Lauten 1995). However, there have been no studies that simultaneously evaluated competing hypotheses about factors (e.g., predation, weather, competitors) that could potentially influence grouse numbers through their effect on survival and reproduction. We used model selection to compare relative support for multiple hypotheses representing potential factors that could influence Ruffed Grouse population fluctuations. Our objective in this study was to revisit a phenomenon (the 10-year grouse cycle) that has been assumed to be resolved scientifically (i.e., predation causes these cycles, Rusch et al. 2000) using the comparative model approach. We believe this approach can be used to guide future research about Ruffed Grouse population cycles.

METHODS

Study Area.—Our study area encompassed a 20,358-km^2 area around Grand Rapids, Minnesota, USA (47° 13′ N, 93° 31′ E), defined by a circle having a radius of 80.5 km. This was the approximate maximum distance traveled from Grand Rapids by hunters who collected grouse for our study. This region was within a transition zone between the deciduous hardwood and boreal forests. The weather was variable over the study period and was characterized by warm, moist summers and cold, snowy winters.

Response Variable.—We were interested in factors that might influence Ruffed Grouse cycles and used spring counts of male Ruffed Grouse drumming displays (a gross index to population fluctuations; Rusch and DeStefano 1989, Zimmerman and Gutiérrez 2007) as our response variable. Male Ruffed Grouse use several displays to attract or court females during the spring, one of which is called the "drumming display" (Rusch et al. 2000:9). This display consists of a male grouse beating its wings in a manner that produces a distinct low frequency nonvocal sound (Rusch et al. 2000). We used data from surveys within the study area that were conducted annually by the Minnesota Department of Natural Resources. Surveys occurred along non-randomly selected, but consistently surveyed, routes that were approximately 14.4 km in length along maintained roads. Wildlife biologists, land managers, and volunteers attempted to survey each route once during the spring (early Apr–early May). Volunteers conducted surveys by stopping every 1.6 km along each route for 4-min intervals to listen for drumming displays. The number of drumming displays heard per 4-min interval was recorded at each stop (Minnesota Department of Natural Resources, unpubl. protocol). Grouse were not surveyed on rainy or windy days. We recognize this index may not truly represent population size and may have represented only drumming display activity of male Ruffed Grouse (Anderson 2001).

Development of a priori Hypotheses.—We evaluated hypotheses (models) about factors that influence Ruffed Grouse population dynamics that exist in the literature (Bump et al. 1947, Gullion and Marshall 1968, Rusch et al. 2000) and our own experience working with grouse. We limited our set of hypotheses to those for which data were available. We considered 13 hypotheses, *a priori* to analysis, which represented predictions about how goshawk abundance, weather during the breeding season, weather during the previous winter, exploitative competition (forest tent caterpillars, *Malacosoma americanum*), color phase ratios, mass of male grouse, and age ratios of both genders during the autumn correlated with Ruffed Grouse population indices that were conducted from 1983 to 2004 (Table 1). We limited our analysis to the interval 1983–2004 because we did not have individual grouse data prior to 1982; the 1982 data were used to predict the population index for the following spring (i.e., spring 1983 counts).

Predation Hypothesis.—Ruffed Grouse are killed by many predators (Bump et al. 1947). Correlative evidence supports a substantial, if not controlling, effect of goshawk and Great Horned Owl predation on the Ruffed Grouse cycle (Keith and Rusch 1989). We did not locate relevant data about Great Horned Owl predation or owl abundance on our study area, but we did acquire population indices of goshawks, which are important predators of Ruffed Grouse in Minnesota (Eng and Gullion 1962). We estimated an annual index of goshawk abundance from counts of migrating raptors at Hawk Ridge Nature Center in Du-

TABLE 1. *A priori* models representing hypotheses of factors correlating with population cycles in Ruffed Grouse in northern Minnesota, USA, 1983–2004.

Model	Verbal hypothesis	Year[a]	Season dates	Variables/Predictions[b,c]
1	Goshawk abundance	T	Fall—Hawk Ridge	$-GH$
2	Freezing while female lays eggs	t–1	20 Apr–15 May	$-DF_l$
3	Cold and wet weather during hatching and brooding	t–1	25 May–25 Jun	$\pm P_h + T_h \pm (P_h{*}T_h)$
4	Negative effects of snow-less cold winter	T	1 Dec–31 Mar	$+T_w + P_w - (T_w{*}P_w)$
5	Duration of extreme cold events	T	1 Dec–31 Mar	$-C_w$
6	Snow depth	T	1 Dec–31 Mar	$+S$
7	Duration of adequate snow cover	T	1 Dec–31 Mar	$+SC$
8	Consecutive years of adequate snow	t–1, t–2, t–3	1 Dec–31 Mar	$+SC + SC_1 + SC_2$
9	Tent caterpillars (cover hypothesis)	t–1	Summer	$-C_1$
10	Tent caterpillars (immediate effect due to loss of buds or production of secondary compounds)	t–1, t–2, t–3	Summer	$-C_1 - C_2 - C_3$
11	Color phase ratios (phenotypic hypothesis)[c]	T	Fall hunt	$\pm GR$
12	Mass of males	T	Fall hunt	$+M_m$
13	Age ratio of both genders—insight into cycles?	t–1	Fall hunt	$\pm A_P$

[a] t = 1 September of previous year to current breeding season.

[b] − = negative correlation, + = positive correlation, ± = effect unknown—could be positive or negative correlation.

[c] P_h = amount of precipitation during the hatching period; T_h = mean minimum daily temperature during the hatching period; P_n = amount of precipitation during the nesting period; DF_l = number of days below freezing during the laying period; T_w = mean minimum temperature during the winter season; P_w = amount of precipitation during the winter season; C_w = number of nights with min temperature below −15° C; S = average daily snow depth during the winter season; SC = number of days with > 15 cm of snow during previous winter (t); SC_1 = number of days with > 15 cm of snow during t–1; SC_2 = number of days with > 15 cm of snow during t–2; GH = index to goshawk abundance: number of goshawks counted at Hawk Ridge; C_1 through C_3 = percent of area within 80.5 km of Grand Rapids with forest tent caterpillar damage; M_m = average mass of immature male grouse from RGS hunt data; A_P = age ratio of both genders (calculated as number of young-of-year birds harvested divided by number of adults harvested) from national hunt; GR = proportion of gray-phased birds harvested during the national hunt.

luth, Minnesota (~110 km from Grand Rapids). Raptor counts were conducted by trained observers from late August through November. Volunteers recorded the number of observation hours and used spotting scopes to record counts of migrating raptors by species. We used these data to estimate the average number of goshawks observed per hour per year as our explanatory variable (model 1, Table 1). We recognize these counts may not reflect predation rates on grouse, but they are similar to indices used in previous studies that correlated grouse abundance with goshawk predation (Keith and Rusch 1989, Lauten 1995).

Weather Hypotheses.—Weather is known to affect both reproduction and survival in gallinaceous birds (Gullion 1970, Moss 1986, Swenson et al. 1994). Thus, we developed seven *a priori* hypotheses about the potential manner in which weather could affect Ruffed Grouse through its effects on reproduction and survival. We organized the weather data into seasons that were biologically relevant to hypotheses about grouse. The primary egg laying period lasted from ~20 April to 15 May, and the hatching/early brood rearing season lasted from ~20 May to 20 June. Spring weather could affect reproduction by affecting the physiological condition of females during the breeding season (Moss 1986). When spring weather conditions reduced reproductive success, fewer males should have been available to display during the following spring (models 2 and 3, Table 1). The winter season (Dec–Mar) has been shown to be stressful to Ruffed Grouse because of low temperatures and the influence of predators (Gullion 1970, Lauten 1995). Specifically, we predicted that precipitation would benefit grouse during cold winters (i.e., increased snow depth for roosting cover), but would negatively influence grouse during warmer winters (i.e., hard crust forms on snow preventing snow roosting; model 4, Table 1). We also predicted that successive periods of extremely cold weather would negatively influence grouse (model 5, Table 1), whereas snow

depth (regardless of snow quality; model 6, Table 1) and long durations of snow cover (models 7 and 8, Table 1) would positively correlate with grouse indices. Winter conditions may also interact with predation to affect survival (Gullion 1973). However, we did not know which specific weather models (i.e., models 4–8) were most appropriate to include in an interaction prior to analysis. We chose not to include a large number of possible interaction models because we wanted to avoid spurious correlations associated with data dredging (Burnham and Anderson 1998).

We used weather data from the Minnesota Climate Working Group (University of Minnesota) for assessing our weather models. Weather data included daily precipitation in cm (as water equivalent when snow fell), snowfall in cm, minimum temperature in °C, and snow depth in cm, which were collected by an automated weather station at Grand Rapids. We calculated the average daily minimum temperature (°C), mean daily precipitation (cm), number of days of snow cover that was adequate for snow roosting (snow depth >15 cm), number of days with extreme low temperatures (minimum temperature <−15° C), and average daily snow depth (cm) for the winter season. We calculated the number of days with a minimum temperature below freezing during the egg-laying season, and the average daily minimum temperature (°C) and mean daily precipitation (cm) during the hatching/brood rearing season.

Competition Hypotheses.—Forest tent caterpillar outbreaks may affect Ruffed Grouse population dynamics (Jakubas and Gullion 1991). Tent caterpillars could have influenced grouse directly by reducing foliage cover (model 9, Table 1) or lowering food supply (i.e., defoliated aspen [*Populus* spp.] trees do not produce catkins, which are the primary winter food for grouse in our study area; model 10, Table 1); or indirectly by causing the defoliated trees to increase production of compounds that discourage defoliation by caterpillars (model 10, Table 1). In the latter case, these compounds either may have made the aspen catkins unpalatable or inhibited digestion of these catkins by grouse. We used data on tent caterpillars collected by the Minnesota Department of Natural Resources' Forest Health Unit and GIS (ArcView 3.2, ESRI Inc., Redlands, CA, USA) to estimate the amount of caterpillar defoliation within the study area for each year of our study. These data contained spatially explicit maps with area polygons representing various categories of tent caterpillar defoliation (i.e., heavy, moderate, light, or none) throughout the entire state of Minnesota. We combined these four categories into two groups: "tent caterpillar outbreaks" (i.e., >20% of an area impacted) and "no tent caterpillar outbreaks" (<20% of an area impacted) for each polygon within the annual GIS layers. We then calculated the proportion of our study area that was defoliated (i.e., "tent caterpillar outbreaks") each year.

Grouse Hypotheses.—Gullion (1970) and Gutiérrez et al. (2003) suggested that survival correlated with color-phases (model 11, Table 1). We also hypothesized that mass of male grouse may correlate with display activity if mass reflected the condition of males entering winter (model 12, Table 1). Finally, we considered whether age ratio of harvested birds reflected overall population momentum (model 13, Table 1). Ruffed Grouse were harvested in the study area by hunters participating in the Ruffed Grouse Society's annual National Grouse and Woodcock Hunt (RGS HUNT) held during the second week of October each year since 1982. We collected morphometric data on all grouse registered during the RGS HUNT (n = 5,700). We estimated the proportion of gray-phased individuals in the population, the age ratio of both genders (calculated as number of young-of-year harvested divided by number of adults harvested), and the average mass of male grouse from the harvested grouse. We considered these estimates to be characteristics of our study population because the RGS HUNT occurred over the entire area. We assumed the Ruffed Grouse harvest data would not be biased for color phase because we knew of no reason, *a priori*, why hunters would take one color phase over another. We assumed that hunters would take a greater proportion of juveniles than existed in the overall population due to age-specific vulnerability (Small 1989). However, we did not believe this bias would change among years, and considered the proportion of juveniles as an index to relative proportion of this segment in the population among years.

Data Analysis.—We used model selection

(Burnham and Anderson 1998) to rank our *a priori* hypotheses about factors that correlated with fluctuations in Ruffed Grouse populations. We first expressed our *a priori* hypotheses as statistical models (Table 1). We then checked for correlations among variables within a model. We used a repeated measures design because grouse were sampled along survey routes each year, and mixed modeling to estimate the parameters for each of our *a priori* models. We used a global model to identify the best covariance structure for the display data. Modeling covariance using this process allowed us to account for correlations between grouse indices among years (i.e., the autocorrelation associated with time series data). We used Akaike's Information Criterion (AIC_c) to rank the models' ability to fit the data, and then estimated the amount of temporal process variation explained by the best (lowest AIC_c) model.

We used PROC CORR in SAS (Version 9.1, SAS Institute Inc., Cary, NC, USA) to develop a correlation matrix of all predictor variables included in the *a priori* hypotheses. If a pair of variables from the same model had a correlation coefficient >0.60, we excluded one variable from the model to avoid multicollinearity. The variable excluded depended upon our subjective assessment of the potential for biological interpretation of each of the two correlated variables.

We used multiple linear mixed modeling (PROC MIXED in SAS) to estimate the parameters of our statistical models. We considered year to be a random effect, predictor variables (i.e., weather, goshawk index, tent caterpillar damage) to be fixed effects, and survey routes as the sampling units. We assumed that routes were independent units within years. We used a repeated measures design to analyze the mixed models because, although routes were independent within years, samples from routes were not independent among years.

The assumptions of linear regression are that error terms are distributed normally and variances are constant. However, estimation techniques based on normal distributions are robust to departures from normality (White and Bennetts 1996). We modeled the variance-covariance structure because we suspected dependence among repeated samples, non-constant variances among years, and autocorrelation of counts through time. We used restricted maximum likelihood and a global model to estimate five variance-covariance structures described by Littell et al. (1996) including first-order autoregressive (AR1), heterogeneous AR1 (HAR1), compound symmetric, unstructured, and log-linear. The AR1 structure assumes that variances are constant among years and that covariances decline with increasing time between observations. The HAR1 is similar to the AR1 structure, but it allows variance estimates to change among years. The compound symmetric assumes homogeneous variance and covariances. The unstructured model assumes that no pattern in variance and covariances exists. The log-linear structure allows flexibility in modeling variances as a function of experimental conditions (e.g., increased variances during years with higher population indices). The autoregressive covariance structures are particularly applicable to cyclic species because they allow observations closer in time to correlate more than observations further away in time. We used standard maximum likelihood estimation (Littell et al. 1996:498) and AIC_c to rank candidate models once we identified the most parsimonious variance-covariance structure. We used the Satterthwaite approximation method for estimating the degrees of freedom for each *a priori* model.

We estimated the amount of variation explained by the AIC_c selected model by first estimating an intercept-only model (i.e., a model containing an intercept parameter with no other fixed effects) and a model containing a variable for each year. The difference in residual variation between these two models represents the total temporal process variation in the population index. Next, we estimated the residual variation from the best annual covariate model. We calculated the percent of temporal process variance explained as the difference in residual variation between the intercept-only model and the best covariate model divided by the total temporal process variation.

RESULTS

Twenty-nine permanent survey routes were sampled within the study area. The number of routes surveyed each year (n = 22 years) var-

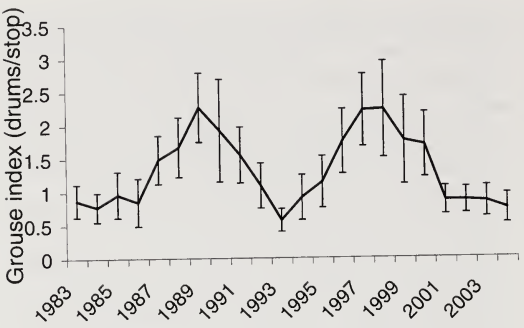


FIG. 1. Plot of Ruffed Grouse population indices (average drums/stop along male display survey routes) collected by the Minnesota Department of Natural Resources from 1983 to 2004, Grand Rapids area, Minnesota, USA. Error bars represent 95% confidence intervals.

ied from 19 to 29 because inclement weather, accessibility of the route, and availability of volunteers to conduct surveys varied by year. The number of times individual routes were surveyed during the entire study varied from 6 to 22. The routes that were surveyed the least were not initiated until 1996–1998, and not all of these newer routes have been surveyed each year since their initiation. The mean number of drums (displays) heard per stop varied from 0.57 in 1993 to 2.27 in 1989. Grouse population indices during our study reflected a ~10-year cyclic pattern (Fig. 1).

Modeling the covariance structure of the Ruffed Grouse population index indicated the data supported a HAR1 structure. This covariance structure included 22 variance estimates (i.e., a variance estimate for each year) and a parameter (ρ) that described the correlation between observations separated by 1 year. This structure indicated that years with higher population indices were characterized by greater variance among survey routes and that indices were correlated from 1 year to the next (ρ = 0.74).

Our data most strongly supported the interaction between winter temperature and precipitation model (model 4, Tables 1–2, Fig. 2). AIC_c weights indicated there was strong support for this model because it was almost three times as likely as the second ranked model. This model indicated that grouse indices were highest during cold snowy and warm dry winters, and lowest following relatively warm snowy and cold dry winters (Fig. 2, Table 3). This interaction model was ranked the highest, but variance components analysis indicated this model only accounted for 17% of the temporal process variation.

DISCUSSION

The Ruffed Grouse cycle has captured the interest of grouse biologists for many years, and has stimulated many studies to investigate its causative mechanisms (Bump et al. 1947, Keith 1963, Gullion 1984, Keith and Rusch 1989, Balzer 1995, Lauten 1995). Rusch et al. (2000) concluded that avian (particularly goshawk) predation was most closely linked to the grouse cycle and, hence, may be the mech-

TABLE 2. Model selection assessing the influence of ecological factors on Ruffed Grouse population indices in northern Minnesota, USA, 1983–2004.

Model	−2 Log likelihood	K[a]	*n*	AIC*c*[b]	Delta AIC*c*	AIC*c* Weight
4	1085.6000	28	532	1144.8286	0.0000	0.4448
3	1087.7000	28	532	1146.9286	2.1000	0.1557
1	1093.4000	26	532	1148.1802	3.3516	0.0833
12	1093.7000	26	532	1148.4802	3.6516	0.0717
11	1093.9000	26	532	1148.6802	3.8516	0.0648
9	1094.5000	26	532	1149.2802	4.4516	0.0480
13	1094.7000	26	532	1149.4802	4.6516	0.0435
6	1095.7000	26	532	1150.4802	5.6516	0.0264
2	1096.5000	26	532	1151.2802	6.4516	0.0177
5	1097.0000	26	532	1151.7802	6.9516	0.0138
7	1097.0000	26	532	1151.7802	6.9516	0.0138
10	1093.4000	28	532	1152.6286	7.8000	0.0090
8	1093.7000	28	532	1152.9286	8.1000	0.0077

[a] K = number of fixed effect, covariance, and variance parameters in models.
[b] AIC*c* = small sample adjustment of Akaike's Information Criterion.

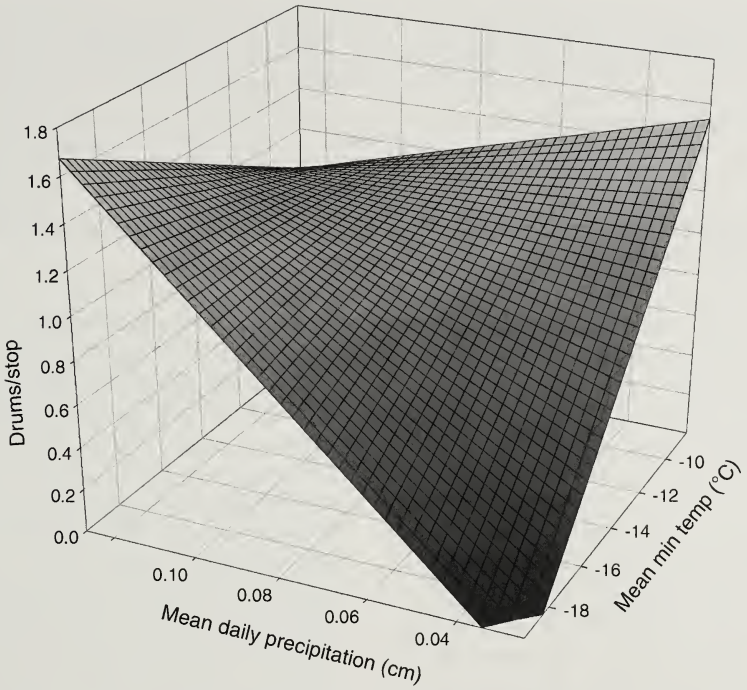


FIG. 2. Predicted effects of interaction between precipitation and temperature on Ruffed Grouse population indices in northern Minnesota, 1983–2004.

anism responsible for these cycles. Predation has been suggested to operate on Ruffed Grouse population cycles in two ways. In the first case, resident predators, particularly raptors, cause grouse cycles when their staple prey (snowshoe hares [*Lepus americanus*]) decline and they switch to grouse, which precipitates the decline of grouse in Canada and Alaska (Keith and Rusch 1989). In the second case, snowshoe hare declines in northern Canada and Alaska may force goshawks to migrate south (Keith and Rusch 1989). When these migrating raptors reach wintering areas in the northern United States, they may increase predation rates on grouse to the point of initiating the decline phase of the grouse cycle (Keith and Rusch 1989, Lauten 1995). The cycle does not gain upward momentum until either snowshoe hares increase and they become the staple prey of raptors or these raptors no longer invade southern areas. The study by Lauten (1995) is particularly compelling because he radio-marked large numbers of birds and recorded substantial mortality from predation. In addition, he showed a negative correlation between the Ruffed Grouse cycle and counts of migrating goshawks (from Hawk Ridge, Whitefish Point Bird Observatory, Wisconsin Christmas Bird Counts, and the Wisconsin Checklist Project; goshawk indices from all raptor count sources were correlated during their study) and Great Horned Owls (from Wisconsin Christmas Bird Counts and Wisconsin Checklist Project). In addition to the negative correlation between grouse and raptor indices, Lauten (1995) also found a positive correlation between the goshawk index, avian predation, and winter mortality rates of Ruffed Grouse. We did not have data on predation rates during our study, but based on the results of our analysis, we speculate that mortality rates of Ruffed Grouse may be buffered by high quality snow roosts (cold and snowy winters) or less energetically stressful winters (warm and dry winters) even when raptor abundance is high (Gullion 1973).

In our analysis, the predation hypothesis was neither a competing model nor explanatory of variation in our grouse population index (drumming display counts). We used goshawk indices similar to those used by Lauten

TABLE 3. Parameter estimates from AIC_c best model (effect of winter temperature, precipitation, and their interaction) for assessing changes in Ruffed Grouse population indices in northern Minnesota, USA, 1983–2004.

Parameter	Estimate	SE	df[a]	95% Confidence interval
Intercept	−0.2782	0.3581	8.53	−1.0950–0.5386
Winter precip	37.0183	10.5500	9.59	13.3651–60.6716
Winter min temp	0.1142	0.0498	7.39	−0.00226–0.2307
Interaction term	−2.9560	1.6443	8.00	−6.7479–0.8358

[a] Estimated using the Satterthwaite procedure in PROC MIXED.

(1995), but found no relationship between grouse and goshawk indices from the previous year, which was used as a surrogate for predation in other studies. Alternatively, the influence of predators may lag due to switching of prey (Tornberg et al. 2005). For example, goshawks may initially prey upon other species (e.g., snowshoe hares) before switching to Ruffed Grouse. We considered this model initially, but did not include it as an *a priori* model because our initial model set was large and we felt there was more support for the non-lag predation hypothesis. Reviewers suggested including this predator lag model and we estimated this model *post hoc* to the analysis. This model performed about equally as well as our original predation model (AIC_c = 1,148.10), but provided no additional explanatory power.

In contrast, we found that winter weather explained the most variation among those hypotheses we considered. Winter weather can influence thermoregulation, cover from predators, and condition of females at the start of the breeding season. Our top model supported the hypothesis that cold, snowy winters favored grouse whereas cold, snow free conditions were unfavorable. However, our top model only explained 17% of the variation in grouse population indices, suggesting that other factors must be important in explaining grouse cycles (e.g., interactions among factors, variation in grouse counts). For example, there could be an interaction between the number of goshawks and snow quantity/quality. Such an interaction may explain the different observations between our study and Lauten (1995) because high quality snow-roosting may provide protective cover during goshawk invasions. Also, there could be interactions between predators, grouse food quality, and snow conditions (Gullion 1970). For example, when forage quality decreases, individual grouse may need to forage for longer periods to find adequate food, which would expose them to predation for longer periods of time (Jakubas and Gullion 1991).

We concluded that goshawk counts (predation hypothesis) by themselves did not explain Ruffed Grouse population cycles within our study area. It was possible that predation was interacting with winter weather conditions in a way that was unknown. Further, we did not evaluate models that hypothesized bottom-up mechanisms for control of cycles. For example, Gullion (1984) hypothesized that food quality changes as a result of intensive foraging on aspen by grouse, which in turn affects either survival or reproduction of grouse. However, Jakubas and Gullion (1991) suggested that food quality alone as manifested by high levels of secondary compounds could not mediate a cycle in Ruffed Grouse. Although weather appeared to correlate with Ruffed Grouse population changes better than some other factors, our study was based on indices of both Ruffed Grouse and goshawk numbers, which could confound our results if the indices did not adequately reflect the population size or ecological interactions (Anderson 2001). In addition, we do not have data on Great Horned Owls, mammalian predators, endogenous factors (Matthiopoulos et al. 2005), or parasites (Mougeot et al. 2005), which may also influence Ruffed Grouse population trends.

Neither Northern Goshawk counts nor winter weather appear to explain population indices (relative fluctuations of grouse numbers based on drumming display counts) for our study population based on our simultaneous evaluation of plausible factors affecting grouse numbers. Thus, we believe the mechanism(s) regulating the Ruffed Grouse cycle (at least in northern Minnesota) is still unknown. We suggest that future studies of

Ruffed Grouse cycles use robust estimators of grouse counts (e.g., Zimmerman and Gutiérrez 2007) and counts of local predators rather than indices to evaluate the influence of predation, weather, habitat and their interactions on Ruffed Grouse population fluctuations.

ACKNOWLEDGMENTS

We thank Jana Albers, A. E. Elling, and M. A. Larson for providing the tent caterpillar data, weather data, and Minnesota DNR Ruffed Grouse display survey data, respectively. We appreciate the assistance of the Grand Rapids Chapter of the Ruffed Grouse Society. F. J. Nicoletti and the Hawk Mountain Bird Observatory provided goshawk data. L. I. Berkeley, L. G. Erickson, and D. D. Grandmaison provided valuable comments on earlier drafts of this manuscript. J. D. Nichols provided valuable discussion during the development of our modeling approach. C. E. Braun, R. E. Kenward, and Patrik Byholm provided valuable comments that improved the quality and clarity of the manuscript. Support for this research was provided by the University of Minnesota, Minnesota Agriculture Experiment Station, Leigh Perkins Fellowship to G. S. Zimmerman, Donald Rusch Fellowship to G. S. Zimmerman, and the Ruffed Grouse Society.

LITERATURE CITED

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Balzer, C. C. 1995. Survival, hunting mortality, and natality of Ruffed Grouse in northwestern Wisconsin. Thesis. University of Wisconsin, Madison, USA.

Bump, G., R. W. Darrow, F. C. Edminster, and W. F. Crissey. 1947. The Ruffed Grouse: life history, propagation, management. New York State Conservation Department, Albany, USA.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference. A practical information-theoretic approach. Springer-Verlag, New York, USA.

Eng, R. L. and G. W. Gullion. 1962. The predation of goshawks upon Ruffed Grouse at the Cloquet Forest Research Center, Minnesota. Wilson Bulletin 74:227–242.

Gullion, G. W. 1970. Factors influencing Ruffed Grouse populations. Transactions of the North American Wildlife and Natural Resources Conference 35:93–105.

Gullion, G. W. 1973. Grouse cycles: are they real? Minnesota Science 29:6–11.

Gullion, G. W. 1984. Grouse of the North Shore. Willow Creek Press, Oshkosh, Wisconsin, USA.

Gullion, G. W. and W. H. Marshall. 1968. Survival of Ruffed Grouse in a boreal forest. The Living Bird 7:117–167.

Gutiérrez, R. J., G. S. Zimmerman, and G. W. Gullion. 2003. Daily survival rates of Ruffed Grouse *Bonasa umbellus* in northern Minnesota. Wildlife Biology 9:351–356.

Jakubas, W. J. and G. W. Gullion. 1991. Use of quaking aspen flower buds by Ruffed Grouse: its relationship to grouse densities and bud chemical composition. Condor 93:473–485.

Keith, L. B. 1963. Wildlife's ten-year cycle. University of Wisconsin Press, Madison, USA.

Keith, L. B. and D. H. Rusch. 1989. Predation's role in the cyclic fluctuations of Ruffed Grouse. International Ornithological Congress 19:699–732.

Lauten, D. J. 1995. Survival, demography, and behavior of Ruffed Grouse of different color phase during a cyclic decline in northwestern Wisconsin. Thesis. University of Wisconsin, Madison, USA.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute Inc., Cary, North Carolina, USA.

Matthiopoulos, J., J. H. Halley, and R. Moss. 2005. Socially induced Red Grouse population cycles need abrupt transitions between tolerance and aggression. Ecology 86:1883–1893.

Mougeot, F., S. A. Evans, and S. M. Redpath. 2005. Interactions between population processes in a cyclic species: parasites reduce autumn territorial behaviour of male Red Grouse. Oecologia 144:289–298.

Moss, R. 1986. Rain, breeding success, and distribution of Capercaillie *Tetrao urogallus* and Black Grouse *Tetrao tetrix* in Scotland. Ibis 128:65–72.

Rusch, D. H. and S. DeStefano. 1989. To tally the grouse. Pages 200–206 *in* Ruffed Grouse (S. Atwater and J. Schnell, Editors). Stackpole Books, Harrisburg, Pennsylvania, USA.

Rusch, D. H., S. DeStefano, M. C. Reynolds, and D. Lauten. 2000. Ruffed Grouse. The birds of North America. Number 515.

Small, R. J. 1989. Tipping the balance. Pages 248–251 *in* Ruffed Grouse (S. Atwater and J. Schnell, Editors). Stackpole Books, Harrisburg, Pennsylvania, USA.

Small, R. J., J. C. Holzwart, and D. H. Rusch. 1991. Predation and hunting mortality of Ruffed Grouse in central Wisconsin. Journal of Wildlife Management 55:512–520.

Swenson, J. E., L. Saari, and Z. Bonczar. 1994. Effects of weather on Hazel Grouse reproduction: an allometric perspective. Journal of Avian Biology 25:8–14.

Tornberg, R., E. Korpimäki, S. Jungell, and V. Reif. 2005. Delayed numerical response of goshawks to population fluctuations of forest grouse. Oikos 111:408–415.

White, G. C. and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. Ecology 77:2549–2557.

Zimmerman, G. S. and R. J. Gutiérrez. 2007. The influence of ecological factors on detecting drumming Ruffed Grouse. Journal of Wildlife Management 71:1765–1792.

The Wilson Journal of Ornithology 120(2):248–255, 2008

COMMUNAL CALLING AND PROSPECTING BY BLACK-HEADED TROGONS (*TROGON MELANOCEPHALUS*)

CHRISTINA RIEHL[1,2]

ABSTRACT.—Many species of trogons (Trogoniformes: Trogonidae) gather in mixed-gender calling assemblages during the breeding season. These assemblages have been compared to leks and are usually assumed to function in mate choice; however, no field data exist to support this hypothesis. I present five non-mutually exclusive hypotheses for the function of mixed-gender calling assemblages and test the predictions using field data from Black-headed Trogons (*Trogon melanocephalus*) in a lowland dry forest in Costa Rica. Adult trogons gathered in mobile assemblages of 3–12 individuals that called frequently and chased one another from perch to perch while moving through the forest. Groups formed at sunrise throughout all stages of the breeding cycle and were not significantly male-biased. Both breeding and non-breeding individuals participated in assemblages, and copulations were not observed in assemblages. Prey capture rates of individuals foraging in groups did not differ from those foraging alone. Males called and chased other individuals more often than did females; however, males chased females and other males at equal rates. Assemblages of trogons frequently prospected (investigated potential nest sites and active nests of conspecifics). These data suggest that communal assemblages of calling trogons do not function solely in social mate choice, nor do they enhance foraging efficiency. They may have a role in maintenance of territorial boundaries and selection of future nest sites. *Received 2 February 2007. Accepted 20 July 2007.*

Trogons (Trogoniformes: Trogonidae) are among the most secretive of tropical forest birds. Many aspects of their behavior, particularly those relating to courtship, mate choice, nesting biology, and social interactions remain poorly understood or undescribed (Johnsgard 2000). Trogons are generally solitary; however, assemblages of calling males have been reported in several species (Table 1). These groups usually consist of 3–10 males, which call repeatedly while chasing each other from perch to perch, and a smaller number of females.

Most observers have reported that calling assemblages contain more males than females and form only in the breeding season, leading to the widespread assumption these groups function in courtship and mate choice (e.g., Skutch 1972, Brosset 1983, Howell and Webb 1995, Johnsgard 2000). These assemblages have been termed "quasi-leks" (Brosset 1983: 8), "noisy leks" (Howell and Webb 1995: 432), and "lek-like assemblages" (Johnsgard 2000:113), but virtually no field data exist to support this hypothesis. No studies of individually color-marked trogons have been performed and the breeding status of individuals in assemblages is usually not known. The behavior is described only from anecdotal observations and no quantitative data exist on the sex ratios of groups or on the behavior of females participating in groups. There are no reports of copulations occurring in assemblages and no information on whether these groups continue to form throughout the breeding season.

There are several reasons to doubt that mate choice occurs in the context of group displays. Unlike polygynous lekking species, trogons are monogamous and territorial; both parents excavate the nesting cavity, incubate the eggs, and feed the nestlings until fledging. In the few species that have been well studied, the male chooses a nest site, begins to excavate it if necessary, and advertises it to females by calling repeatedly (Skutch 1983, Hall and Karubian 1996, Johnsgard 2000). The quality of the nest site and territory, therefore, appears to be an important component of female choice. Males remain territorial throughout the breeding season, often advertising their territories by calling in synchrony with males in adjacent territories. The few recorded instances of trogons copulating have occurred at the nest site with no extra-pair individuals present (Slud 1964, Hall and Karubian 1996). Finally, calling assemblages are mobile; indi-

[1] Museum of Comparative Zoology, Harvard University, 24 Oxford Street, Cambridge, MA 02138, USA.

[2] Current address: Department of Ecology and Evolutionary Biology, Princeton University, 106A Guyot Hall, Princeton, NJ 08544, USA; e-mail: criehl@princeton.edu

TABLE 1. Group size and composition of the 10 trogon species reported to form calling assemblages.

Species	Group size and composition[a]	Source
Eared Quetzal (*Euptilotis neoxenus*)	2 M, 1 F	Zimmerman 1978
Hispaniolan Trogon (*Priotelus roseigaster*)	6[b]	Wetmore and Swales 1931
Choco Trogon (*Trogon comptus*)		Häffer 1975
Black-headed Trogon (*T. melanocephalus*)	≤10 M[c]	Howell and Webb 1995
Amazonian White-tailed Trogon (*T. viridis*)	"several M"	Johnsgard 2000
Citreoline Trogon (*T. citreolus*)	≤10 M[c]	Howell and Webb 1995
Slaty-tailed Trogon (*T. massena*)	"several"[b]	Skutch 1972
Violaceous Trogon (*T. violaceus*)	"a number"[b]	Skutch 1972
Narina Trogon (*Apaloderma narina*)	≤7 M[c]	Brosset 1983
Bare-cheeked Trogon (*A. aequatoriale*)	≤6 M[c]	Brosset 1983

[a] M = male, F = female.
[b] No information available on sex ratio.
[c] Unspecified number of females also present.

viduals move together as a group rather than gathering and displaying at a fixed arena (Cunningham van-Someren 1973, Brosset 1983, Johnsgard 2000).

The hypothesis that communal calling assemblages function in social mate choice generates the following predictions: (1) assemblages should form most frequently at the onset of the breeding season, prior to egg-laying; (2) individuals that are tending nests should not participate in calling assemblages; (3) males should call more frequently than females; and (4) the sex ratio of assemblages should be male-biased.

Alternatively, group calling assemblages could serve one or more of several functions. These hypotheses are not mutually exclusive, but do generate different predictions concerning timing of group formation, behavior of males and females, and presence of breeding individuals in assemblages.

Extra-pair Mate Choice.—Communal calling assemblages are unlikely to have a role in social mate choice, but they could provide an opportunity for already-mated trogons to gain extra-pair copulations. Recent molecular analyses of paternity have revealed the majority of socially monogamous birds are genetically promiscuous; in fact, true genetic monogamy is the exception rather than the rule (Griffith et al. 2002). This hypothesis predicts that: (1) assemblages should form throughout the breeding season; (2) males should call and chase more frequently than females; (3) males should chase females more often than other males; and (4) females that are tending young should not participate in assemblages, whereas males that are tending young should participate.

Foraging Benefits.—Trogons in groups might forage more efficiently than lone individuals if groups are better able to locate prey, watch for predators, exclude interspecific competitors from foraging areas, or invade territories defended by lone pairs (Alexander 1974, Clark and Mangel 1986). This hypothesis does not predict behavioral differences among males and females in calling assemblages, but it does predict that: (1) assemblages should not be restricted to the breeding season; (2) foraging efficiency (prey capture rate) should be higher for individuals in groups than for lone individuals; and (3) both breeding and non-breeding individuals should participate in assemblages.

Nest-site Prospecting.—Individuals might assemble into groups to investigate potential nest sites and active nests of conspecifics if predation risk is lowered or if individuals benefit by following other individuals and sharing information (Patterson and Makepeace 1979). This hypothesis predicts that: (1) assemblages should form throughout the breeding season; (2) groups should be observed investigating potential nest sites; and (3) groups should be composed primarily of non-breeding individuals.

Maintenance of Territorial Boundaries.—Communal displays might provide an opportunity for pairs to advertise their presence to their neighbors and to re-enforce territorial boundaries. If so, (1) assemblages should

form throughout the breeding season; (2) males should call and chase more frequently than females; (3) males should chase males more often than females; and (4) groups should be composed primarily of breeding individuals.

In this paper, I document mixed-gender calling assemblages in a breeding population of Black-headed Trogons (*Trogon melanocephalus*) in a lowland dry forest in Costa Rica, and use field observations to test hypotheses for the adaptive benefits of communal calling in this species. Black-headed Trogons form assemblages of up to 10 individuals of both genders during the breeding season (Howell and Webb 1995), but little is known of the reproductive behavior of the species aside from anecdotal accounts of such groups. Skutch's (1948) study, based primarily on observations at a single nest, remains the most thorough account of the natural history of this species. I monitored 14 Black-headed Trogon nests, followed foraging individuals, and recorded assemblages of calling trogons during one breeding season, June–August 2004. I recorded the total number of individuals in each group, the number of males and females, instances of prospecting behavior, calling rates, and prey capture rates of focal individuals of both genders and, when possible, the breeding status of individuals.

METHODS

Parque Nacionál Santa Rosa (SRNP) is a semi-forested 10,800-ha preserve on the Pacific coastal plain of northwestern Guanacaste Province, Costa Rica (10° 45′ 11° 00′ N, 85° 30′–45′ W) and is part of the 120,000-ha Area de Conservación Guanacaste (ACG). Lowland dry forest predominates, which is highly seasonal and largely deciduous (Janzen 1988). I located and monitored 14 Black-headed Trogon nests by walking trails and transects through the SRNP, listening for calling trogons, and searching for potential nest sites (cavities in arboreal *Nasutitermes* termitaria). Nests were observed from either a concealed place or a blind at least 20 m from the nest. Each nest with chicks was observed for a minimum of 11 hrs and I followed foraging adults from 10 of the 14 nesting pairs (focal animal sampling; Altmann 1974). Each focal adult was observed for a minimum of 15 hrs; observation time was equally divided between morning (0530–1200 hrs CST) and afternoon (1200–1830 hrs CST) periods.

Black-headed Trogons often gather in mobile assemblages of 3–12 individuals that perch in the same or adjacent trees, call frequently, and chase one another from perch to perch (Howell and Webb 1995, Johnsgard 2000). I often encountered these groups while following focal adults and while locating singing trogons at sunrise. I recorded the time of day for each encounter, time since sunrise, date, total group size, number of individuals of each gender, reproductive status of individuals (if known), calling rates of focal individuals, and prey capture rates of focal individuals. Breeding individuals could often be identified by distinctively damaged rectrices (which become frayed and bent to one side while incubating or brooding in the nesting cavity). When one individual flew at another and supplanted it on a perch, I recorded the gender of both birds. Group members did not assemble at fixed sites, but traveled slowly together through the forest. I followed groups on foot until they dispersed and used a handheld GPS unit to record the total distance traveled by the group (path length) as well as the net distance traveled. Groups were considered to have dispersed when ≤ two individuals remained in the same tree or when ≤ one individual continued to vocalize. I used the ArcView extension programs ANIMAL MOVEMENT and SPATIAL ANALYST to project coordinates into UTMs, and to calculate total distances and net distances traveled by assemblages (ArcView Projection Utility Wizard; Hooge and Eichenlaub 1997).

I recorded trogons investigating potential nest sites and active nests while observing nests, lone individuals, and calling groups. Prospecting birds were identified following Doligez et al. (2004): (1) presence of extrapair individuals near active nests, identified by molt patterns and/or feather wear; (2) simultaneous presence of two individuals of the same gender near active nests; (3) observations of individuals repeatedly inspecting contents of a nest from the entrance of the cavity without entering; or (4) observations of individuals perching on and/or pecking potential nest sites (unexcavated termitaria). Several of these criteria often occurred together.

All data were tested for normality (Kolmogorov-Smirnov goodness-of-fit test) and nonparametric tests were used when data were not normally distributed. I used log-likelihood *G*-tests to test for effect of time of day on the probability of observing assemblages. I used linear regressions with *F*-tests for significance to examine the effect of date on assemblage size and on the probability of observing assemblages (Zar 1999). I used replicated *G*-tests to test for heterogeneity and goodness-of-fit to a sex ratio of unity (Sokal and Rohlf 1995) to examine whether calling assemblages consisted of equal numbers of males and females. Chasing data (incidences of a focal individual supplanting another individual on a perch) were converted to rates (chases/min) for each observation period. All pair-wise combinations (male supplanting male, male supplanting female, female supplanting male, and female supplanting female) were compared using ANOVA. I used a Mann-Whitney *U*-test to examine whether calling rates differed between focal males and females in groups, and a *t*-test to examine whether prey capture rates differed between focal individuals foraging alone and those in groups. All tests were two-tailed and results were considered significant at $\alpha = 0.05$. Analyses were conducted with SPSS 12.0 (2003).

RESULTS

I encountered 25 calling assemblages of Black-headed Trogons in 79 days (677 hrs) of observations of nests and focal adults. Assemblages were more likely to be observed during morning than afternoon periods (log-likelihood *G*-test, $G = 20.72$, df = 1, $P < 0.001$); all but two assemblages were observed in the early morning soon after sunrise (assembly, $\bar{x} \pm$ SD = 62 ± 27 min after sunrise; dispersal, $\bar{x} = 134 \pm 39$ min after sunrise). Group size ranged from 3 to 12 individuals ($\bar{x} \pm$ SD = 5.6 ± 2.4). There was no difference in average number of adult males and females in the assemblages (male, $\bar{x} \pm$ SD = 3.45 ± 1.28 individuals/group; female, $\bar{x} = 2.05 \pm 0.94$ individuals/group; replicated *G*-tests; $G_T = 13.77$, df = 25, $P = 0.98$).

Assemblages of Black-headed Trogons did not gather at fixed sites; members of a group moved slowly together through the forest for up to 1,300 m before dispersing (path length $\bar{x} \pm$ SD = 870 ± 340 m; net distance $\bar{x} = 562 \pm 299$ m). Groups were fairly cohesive; all individuals usually stayed in the same or adjacent trees, often in the crown of a large canopy tree (*Enterolobium, Spondias*, *Pithecellobium*). Both males and females in the groups foraged gleaning caterpillars and other insects from the canopy foliage, and called continually.

Calling assemblages were observed during all 3 months of the study period. Date had no effect on frequency of assemblages ($r^2 = 0.0046$, df = 11, $F_{1,10} = 0.046$, $P = 0.83$; Fig. 1A), or on group size ($r^2 = 0.0014$, df = 25, $F_{1,24} = 0.033$, $P = 0.86$; Fig. 1B). Both breeding and non-breeding adults participated in assemblages; at least 9 of 25 groups (36%) contained one or more individuals known to be tending nests ($\bar{x} = 0.44 \pm 0.65$ breeding individuals per group). Not all breeding adults could be identified and these values are conservative.

Focal males chased other individuals from perch to perch significantly more often than did focal females (ANOVA, $F_{3,76} = 15.52$, $P < 0.001$; Fig. 2). However, males were not significantly more likely to chase other males than females (ANOVA, $F_{1,38} = 0.049$, $P = 0.83$; Fig. 2). Focal males in assemblages also called more often than did focal females (Mann-Whitney $U = 128$, $P < 0.001$). On average, prey capture rates for focal individuals foraging in groups ($\bar{x} \pm$ SE = 1.03 ± 0.18 captures/min) did not differ from those foraging alone ($\bar{x} = 0.94 \pm 0.13$; *t*-test, $t_{38} = 0.405$, $P = 0.69$; Fig. 3).

I observed trogons prospecting in groups (investigating neighboring nests and potential nest sites) on 12 occasions (Table 2). Prospectors included birds of both genders that were attending nests ($n = 4$ individuals) as well as birds of unknown reproductive status ($n = 71$). Most observations were of trogons investigating potential nest sites (arboreal *Nasutitermes* termite nests) that were not excavated ($n = 10$). In addition, extra-pair trogons were observed looking into occupied nests ($n = 2$). Lone trogons also prospected ($n = 9$ individuals: 5 males of unknown reproductive status, 3 females of unknown reproductive status, and 1 breeding female).

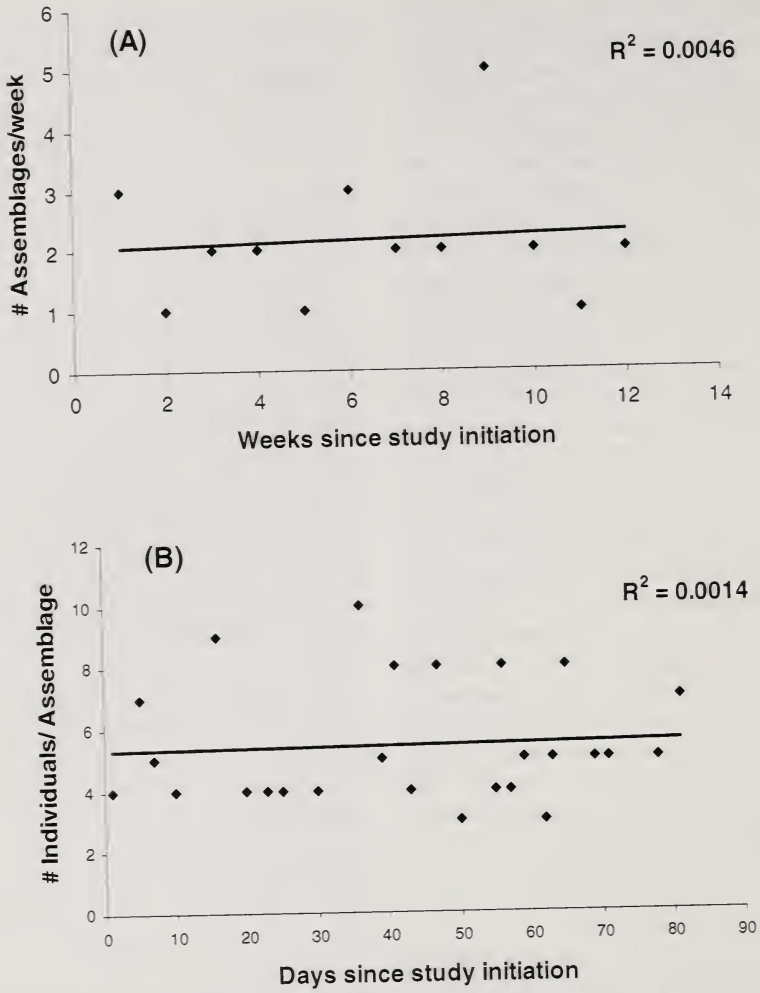


FIG. 1. Frequency and size of assemblages of Black-headed Trogons in Parque Nacionál Santa Rosa, Costa Rica, June–August 2004 (n = 26 assemblages). (A) Relationship between number of assemblages observed per week and study week (P = 0.83). (B) Relationship between number of trogons per assemblage and date of observation (P = 0.86).

DISCUSSION

It has been proposed that mixed-gender assemblages of Black-headed Trogons function primarily in social mate choice. I found only one of four predictions of this hypothesis to be supported. Groups were not significantly male-biased and generally comprised several individuals of both genders. Both breeding and non-breeding birds participated in assemblages, and assemblages continued to form throughout the breeding season, well past the laying date of the known active nests in the study area. Males called and chased other individuals more often than did females. Males chased females and other males with equal frequency, making it difficult to ascertain if chases represent courtship or simply aggression. These data indicate that mixed-gender assemblages have some function aside from social mate choice, and may be entirely unrelated to pair-bond formation.

Many of my data are consistent with the hypothesis that calling assemblages could function in extra-pair mate choice; both breeding and non-breeding males were observed in assemblages, and males called and chased other individuals more often than did females. However, females tending nests also partici-

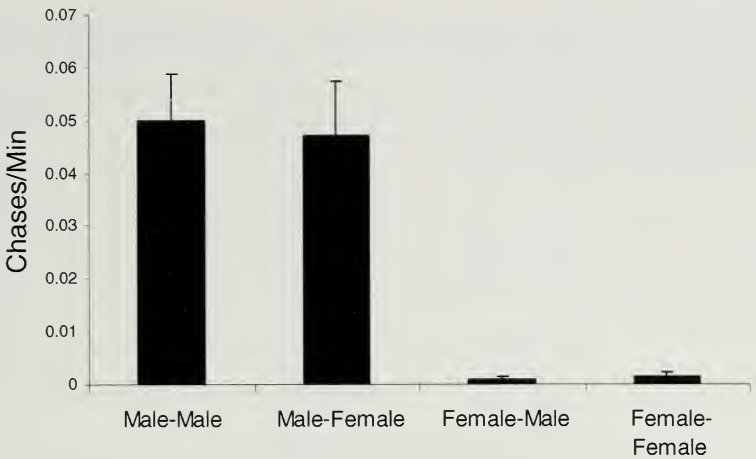


FIG. 2. Mean number (+ SE) of times/min/observation period (n = 20 observation periods, 640 min total) that male and female Black-headed Trogons chased other individuals in assemblages (Parque Nacionál Santa Rosa, Costa Rica, Jun–Aug 2004). Columns represent, from left to right, males chasing males, males chasing females, females chasing males, and females chasing females.

pated in calling assemblages and copulations did not occur in assemblages. It is not likely that assemblages facilitate efficient foraging; groups formed only in the breeding season and trogons foraging in groups did not have significantly higher prey capture rates than those foraging alone.

I found substantial support for the hypothesis that mixed-gender assemblages of Black-headed Trogon may have a role in habitat assessment and selection of future nest sites. Black-headed Trogons do not nest cooperatively, but breeding and non-breeding individuals prospected for nest sites both individually and as part of larger groups. Prospecting groups of trogons visited potential nesting sites (unexcavated termitaria) and active nests, perching on, looking into, and even entering the nesting cavities of other breeding pairs of trogons. Prospecting is relatively infrequent and difficult to recognize in the field, and has traditionally received little attention from behavioral ecologists. A mounting body of evidence suggests that, in some species, pros-

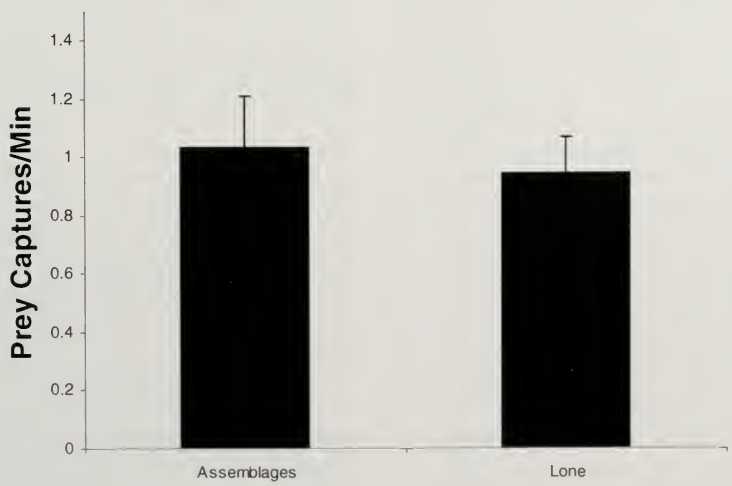


FIG. 3. Mean number (+ SE) of prey captures/min/observation period for focal Black-headed Trogons foraging in assemblages and alone (Parque Nacionál Santa Rosa, Costa Rica, Jun–Aug 2004) (n = 20 observation periods, 640 min total for each category).

TABLE 2. Prospecting by groups of Black-headed Trogons (n = 12 prospecting events) in Parque Nacionál Santa Rosa, Costa Rica, 2004.

Date	Number of males in group	Number of females in group	Status of termitarium being investigated	Reproductive status of prospecting birds[a]
09 Jun	3	2	Unoccupied	Unknown
15 Jun	4	4	Unoccupied	1 br male, 7 unknown
23 Jun	3	3	Unoccupied	Unknown
27 Jun	4	1	Unoccupied	Unknown
04 Jul	4	3	Unoccupied	2 br male, 7 unknown
10 Jul	5	3	Unoccupied	Unknown
21 Jul	3	4	Unoccupied	Unknown
24 Jul	1	1	Occupied (chicks)	Unknown
07 Aug	3	2	Unoccupied	1 br female, 4 unknown
18 Aug	4	4	Occupied (chicks)	Unknown
26 Aug	6	3	Unoccupied	Unknown
29 Aug	1	2	Unoccupied	Unknown

[a] br = breeding; tending either eggs or chicks.

pecting has an important role in the dynamics of dispersal and habitat use within a population, and is more widespread than previously thought (Boulinier et al. 1996, Reed et al. 1999). Studies in the temperate zone have found that prospecting birds gather while investigating nearby nest sites, which influences their choice of future nest sites (Zicus and Hennes 1989, Pärt and Doligez 2003, Doligez et al. 2004). The study of prospecting behavior in tropical birds is still in its infancy and group prospecting has been reported in only a few species (Patterson and Makepeace 1979, Eadie and Gauthier 1985).

It is also possible that calling assemblages allow breeding adults (particularly males) to delineate and reinforce territorial boundaries between adjacent territories. The hypothesis that group displays function in maintenance of territories is supported by the findings that males in assemblages chased other individuals more often than did females, and chased individuals of both genders. Males in assemblages also called more frequently than did females; individual males at the nest advertised their territories by calling in synchrony with males in adjacent territories (with as many as 4 males calling simultaneously; CR, unpubl. data). Males from neighboring territories were also observed mobbing potential nest predators together; five males gathered in response to alarm calls at one nest (CR, unpubl. data).

Calling assemblages usually formed at or immediately after sunrise, raising the possibility that function of communal calling in trogons is similar to that of the dawn chorus of passerines. Like trogon assemblages, the dawn chorus was originally thought to have a role in mate attraction; however, dawn singing also extends throughout the breeding season and may also function in territory defense (Staicer et al. 1996). Prospecting individuals might use a dawn chorus to assess singing residents and territory occupancy; non-territorial male Common Nightingales (*Luscinia megarhynchos*), for example, prospect for territories primarily in the hour before sunrise, when singing by resident males is at a peak (Amrhein et al. 2004). Chorusing and prospecting may both peak at dawn if foraging is less profitable at this time of day. Alternatively, non-territorial individuals may find it most informative to prospect for vacant territories at a time when most resident males are singing (Hutchinson 2002, Amrhein et al. 2004). Non-territorial trogons might therefore use dawn calling assemblages to assess the status of occupied nests and prospect for potential nest sites, whereas resident trogons might call to advertise their presence and defend their territories against floaters and neighboring territory holders.

Future studies of communal calling in trogons should confirm the breeding status and age class of individuals participating in assemblages, and should investigate the effect of prospecting behavior on future nest site selection and reproductive success. Observations of color-marked birds are needed to as-

certain whether groups are composed of the same individuals that gather to display day after day, or whether groups also include nonterritorial floaters.

ACKNOWLEDGMENTS

I thank D. H. Janzen, J. R. Trimble, D. S. Causey, J. A. Klemens, S. J. Agosta, the staff of Parque Nacionál Santa Rosa, and the Museum of Comparative Zoology at Harvard University for logistical support. J. O. Coulson, T. D. Coulson, and two anonymous reviewers provided invaluable advice and comments on the manuscript. I am grateful to the Harvard College Research Program for providing funding for this project.

LITERATURE CITED

Alexander, R. A. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics 5:325–383.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Amrhein, V., H. P. Kunc, and M. Naguib. 2004. Nonterritorial nightingales prospect territories during the dawn chorus. Proceedings of the Royal Academy of Sciences Series B (Supplement) 271: S167–S169.

Brosset, A. 1983. Parades et chants collectives chez les couroucous du genre *Apaloderma*. Alauda 51: 1–10.

Boulinier, T., E. Danchin, J.-Y. Monnat, C. Doutrelant, and B. Cadiou. 1996. Timing of prospecting and the value of information in a colonial breeding bird. Journal of Avian Biology 27:252–256.

Clark, C. W. and M. Mangel. 1986. The evolutionary advantages of group foraging. Theoretical Population Biology 30:45–75.

Cunningham van-Someren, G. R. 1973. Calling and flight display assembly in male trogons. Bulletin of the East African Natural History Society 81: 117–260.

Doligez, B., T. Pärt, and E. Danchin. 2004. Prospecting in the Collared Flycatcher: gathering public information for future breeding habitat selection? Animal Behaviour 67:457–466.

Eadie, J. M. and G. Gauthier. 1985. Prospecting for nest sites by cavity-nesting ducks of the genus *Bucephala*. Condor 87:528–534.

Griffith, S. C., I. P. F. Owens, and K. A. Thuman. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Molecular Ecology 11:2195–2212.

Häffer, J. 1975. Avifauna of northwestern Colombia, South America. Bonner Zoologische Monographien 7:1–182.

Hall, L. S. and J. O. Karubian. 1996. Breeding behavior of Elegant Trogons in southeastern Arizona. Auk 113:143–150.

Hooge, P. N. and B. Eichenlaub. 1997. Animal movement extension to Arcview, Version 1.1. USGS, Alaska Biological Science Center, Anchorage, USA.

Howell, S. N. G. and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press, New York, USA.

Hutchinson, J. M. C. 2002. Two explanations of the dawn chorus compared: how monotonically changing light levels favor a short break from singing. Animal Behavior 64:527–539.

Janzen, D. H. 1988. Ecological characterization of a Costa Rican dry forest caterpillar fauna. Biotropica 20:120–135.

Johnsgard, P. A. 2000. Trogons and quetzals of the world. Smithsonian Institution Press, Washington, D. C., USA.

Pärt, T. and B. Doligez. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. Proceedings of the Royal Society of London, Series B, 270:1809–1813.

Patterson, I. J. and M. Makepeace. 1979. Mutual interference during nest prospecting in the Shelduck, *Tadorna tadorna*. Animal Behaviour 27: 522–535.

Reed, J. M., T. Boulinier, E. Danchin, and L. W. Oring. 1999. Informed dispersal: prospecting by birds for breeding sites. Current Ornithology 15: 189–259.

Skutch, A. F. 1948. Life history of the Citreoline Trogon. Condor 50:137–147.

Skutch, A. F. 1972. Studies of tropical American birds. Publications of the Nuttall Ornithological Club, Number 10. Nuttall Ornithological Club, Cambridge, Massachusetts, USA.

Skutch, A. F. 1983. The birds of tropical America. University of Texas Press, Austin, USA.

Slud, P. 1964. The birds of Costa Rica: distribution and ecology. Bulletin of the American Museum of Natural History 128:1–430.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York, USA.

SPSS Institute Inc. 2003. SPSS for Windows. Version 12.0. SPSS Institute Inc., Chicago, Illinois, USA.

Staicer, C. A., D. A. Spector, and A. G. Horn. 1996. The dawn chorus and other diel patterns in acoustic signaling. Pages 426–453 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Editors). Cornell University Press, Ithaca, New York, USA.

Wetmore, A. and B. H. Swales. 1931. The birds of Haiti and the Dominican Republic. Bulletin of the U. S. National Museum 155:1–483.

Zar, J. H. 1999. Biostatistical analysis. Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zicus, M. C. and S. K. Hennes. 1989. Nest prospecting by Common Goldeneyes. Condor 91:807–812.

Zimmerman, D. A. 1978. Eared Trogon—immigrant or visitor? American Birds 32:135–139.

The Wilson Journal of Ornithology 120(2):256–267, 2008

SONG VARIATION IN BUFF-BREASTED FLYCATCHERS (*EMPIDONAX FULVIFRONS*)

M. ROSS LEIN[1]

ABSTRACT.—I examined song variation within and among 23 individual Buff-breasted Flycatchers (*Empidonax fulvifrons*) recorded in the Chiricahua and Huachuca mountains of Arizona in 1999. I recorded two distinct song types from each individual during intense pre-dawn singing. I used both spectrographic cross correlation (SPCC) of entire songs and discriminant function analysis (DFA) of temporal and frequency measurements to examine whether songs were individually distinctive, and whether songs differed between the two localities. Similarity values of pairs of songs from SPCC were significantly greater for within-male than for between-male comparisons for both song types. Mean similarity values for the two song types did not overlap between these comparison categories. Similarity values between songs of pairs of males from the same mountain range were not greater than for comparisons between pairs of males from different ranges. All temporal and frequency measures for both song types varied significantly more among than within individuals. DFA of principal component scores derived from these measures assigned 85% of Type 1 and 86% of Type 2 songs to the correct individual. Only three frequency variables measured from Type 1 songs differed significantly between birds from the two mountain ranges. DFA assigned only 61% of songs of either type to the correct mountain range, not significantly greater than expected by chance. Thus, both techniques demonstrate significant individual distinctiveness in songs of this species, and neither suggests any geographic structuring of song variation between the two mountain ranges. However, SPCC is considerably more efficient and has greater potential to assign unknown recordings to known individuals correctly, and to detect recordings of "new" individuals not included in the reference sample. *Received 24 April 2007. Accepted 19 July 2007.*

Most literature on song variation deals with oscine birds (Passeriformes, suborder Passeri) (Lovell and Lein 2004). Songs are learned in most or all oscines (Kroodsma 1996), which is a major factor generating song variation at individual, population, and geographic scales. Suboscine birds (suborder Tyranni) appear to show lower levels of song variation. The absence of learning during song ontogeny has been demonstrated for a few species of North America tyrant flycatchers (Tyrannidae) (Kroodsma 1996), and this has been generalized to all suboscines based primarily (and circumstantially) on the limited variation in their songs relative to oscines.

Early studies used song variation in suboscine passerines to help resolve the taxonomic status of populations (e.g., Stein 1963; Johnson 1963, 1980; Lanyon 1978) or described how song variants were used in communication systems (Smith 1969, 1970, 1988). None of these studies focused explicitly on the nature of song variation among individuals within local populations. Song variation among individuals, albeit minor, is apparent in published spectrograms of a variety of suboscine species (e.g., Stein 1963, Payne and Budde 1979, Kroodsma 1984). However, in contrast to the large, often qualitative, differences which may be obvious in spectrograms of different individuals (e.g., Borror 1960) or populations (e.g., Baptista and King 1980) of oscines, examination of suboscine song variation requires quantitative analysis of sufficiently large samples of recordings. The few analyses conducted to date have demonstrated, for example, that songs of Alder Flycatchers (*Empidonax alnorum*) (Lovell and Lein 2004) and Acadian Flycatchers (*E. virescens*) (Wiley 2005) are individually distinctive, and that songs of the endangered Southwestern Willow Flycatcher (*E. traillii extimus*) differ significantly from those of a neighboring subspecies (*E. t. adastus*) (Sedgwick 2001). However, more studies are needed to demonstrate the generality of such patterns, especially for other groups of suboscines.

Most quantitative studies of song variation have used univariate or multivariate analyses of temporal and frequency characters measured from spectrograms. Characters are usually selected on the basis of their ease of measurement with the assumption that if enough characters are measured, the analysis will cap-

[1] Department of Biological Sciences, University of Calgary, Calgary, AB T2N 1N4, Canada; e-mail: mrlein@ucalgary.ca

ture the features that may be important. However, it is often difficult to select characters that can be measured in an objective manner for all songs, and characters are often extremely general (e.g., number of notes, maximum frequency, etc.), capturing little of the "structure" of the vocal signal.

Digital processing of acoustic signals provides alternative methods for characterizing variation among songs. Peter Marler and coworkers (Clark et al. 1987) first used spectrographic cross correlation (SPCC) to characterize variation in notes of songs of Swamp Sparrows (*Melospiza georgiana*). SPCC compares two digital spectrograms at successive offsets on the time axis and calculates normalized covariance (ranging from −1 to 1) at each offset. The maximum covariance is used as a measure of similarity between the two signals (Baker and Logue 2003). SPCC has the advantage that distribution of sound energy in both frequency and time are compared in a "holistic" manner, probably capturing more of the relevant features of the song than would a small number of quantitative measurements (Khanna et al. 1997). Several bioacoustical analysis software packages include routines that automate such measurements. The CORMAT routine of the SIGNAL digital signal analysis software (Engineering Design, Berkeley, CA, USA) can run SPCC on samples of up to 200 songs simultaneously.

The Buff-breasted Flycatcher (*Empidonax fulvifrons*) is the least known of the 11 species of this genus that breed in Canada or the United States (Bowers and Dunning 1994). It breeds in montane forests through Mexico south to Guatemala, El Salvador, and Honduras (AOU 1998), but has been studied almost exclusively in extreme southeastern Arizona where small numbers of birds, possibly less than 100 pairs in total (Martin 1997), inhabit several isolated mountain ranges. I recorded songs of male Buff-breasted Flycatchers during 1999 in the Chiricahua Mountains and the Huachuca Mountains, the two ranges with the largest populations of this species in Arizona.

Male Buff-breasted Flycatchers use two distinctive song types, which I designate as Type 1 and Type 2, during pre-dawn singing and during strong daytime singing (Fig. 1). Bowers and Dunning (1994) published spectrograms of Type 1 songs, which they describe as "chee-lick", but did not describe or illustrate the Type 2 song. Type 2 songs are rarely used during the sporadic daytime singing typical of the breeding cycle following pairing. They are similar to Type 1 songs in sound, but the higher frequency is obvious to the ear.

My objective was to characterize patterns of song variation within and among individuals in the Chiricahua and Huachuca mountains. I conducted both spectrographic cross-correlation and multivariate analyses of song characters for the same sample of songs to answer two questions. First, are songs of Buff-breasted Flycatchers individually distinctive? Second, are there detectable differences in songs of birds between the two mountain ranges?

METHODS

Study Area and Field Methods.—I recorded 23 individual male Buff-breasted Flycatchers at seven sites in two isolated mountain ranges in southeastern Arizona between 7 and 25 June 1999. Specific recording localities in the Chiricahua Mountains (number of individuals in parentheses) included Cave Creek (3), Pinery Canyon (2), Rucker Canyon (6), and West Turkey Creek (2). Localities in the Huachuca Mountains were Carr Canyon (3), Garden Canyon (1), and Sawmill Canyon (6). Males at West Turkey Creek and Sawmill Canyon were recorded on multiple dates whereas individuals at other sites were recorded only on one or two dates. Buff-breasted Flycatchers breed in open woodlands dominated by pines (*Pinus* spp.), live oaks (*Quercus* spp.), and alligator juniper (*Juniperus deppeana*). Sites within the same mountain range were separated by maximum distances of 22 km (Chiricahua) and 7 km (Huachuca), whereas breeding populations in the two mountain ranges are separated by more than 100 km of unsuitable desert habitat. Birds arrived on territories in mid-April and paired immediately. However, nesting did not begin until late May. Most pairs were involved in nest-building or egg-laying during the period of recording.

Recordings of pre-dawn singing were made between 0436 and 0518 hrs MST using a Sony TCD-D10 ProII DAT recorder and a Telinga ProII parabolic microphone, or a Sony TC-D5 ProII cassette recorder and a Audio-

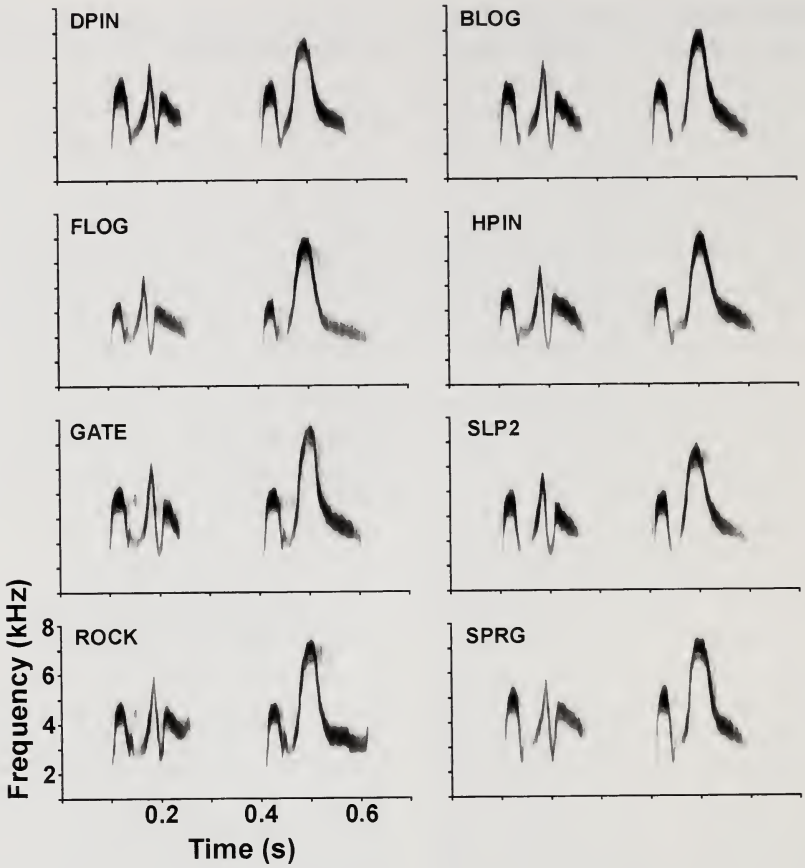


FIG. 1. Audiospectograms of songs of Buff-breasted Flycatchers. Each panel contains examples of Type 1 and Type 2 songs for an individual male. The four males in the left column are from the Chiricahua Mountains and those in the right column are from the Huachuca Mountains, Arizona.

Tech AT815a "shotgun" microphone. I used recordings of pre-dawn singing because each male sang strongly for 15–20 min prior to dawn each day, even during phases of the breeding cycle when daytime singing was rare and sporadic. Males used relatively low perches during pre-dawn singing and could be approached quite closely; recordings made at this time were of high quality.

Males at West Turkey Creek and Sawmill Canyon were banded and color-marked for individual identification; males at other sites were unmarked. However, such markings were not visible before the end of pre-dawn singing. Misidentification of males was highly improbable because there were few individuals at any site and males on neighboring territories could be heard clearly while recording pre-dawn singing of individuals.

Processing of Recordings.—Recordings were acquired as digital files using RTSD Version 2.0 bioacoustical analysis software (Engineering Design, Berkeley, CA, USA) with a sample rate of 20,000 Hz and 16-bit amplitude resolution. Analog signals were filtered during acquisition with a Krohn-Hite Model 3550 filter to avoid aliasing. I selected single recordings for each individual for subsequent sampling based on high signal-to-noise ratios and adequate numbers of songs. Eight examples of each song type were extracted as individual sound files from each recording using SIGNAL 4.0 bioacoustical analysis software (Engineering Design, Berkeley, CA, USA). Many recordings contained hundreds of songs and I selected samples in quasi-random manner. Only one song of each type was selected from each 20-sec segment of the recording with a

high signal-to-noise ratio. One or more segments were skipped between each segment from which songs were selected if more than eight segments met the criterion. I selected songs within each 20-sec segment with minimal amounts of reverberation or background noise. SIGNAL 4.0 was used to band-pass filter sampled songs, removing noise outside the frequency range of interest (1,500–7,000 Hz for Type 1 songs and 1,500–8,000 Hz for Type 2 songs), and to normalize all sampled songs to the same root-mean-square amplitude.

Use of single recordings for each individual may underestimate the amount of variation in songs within individuals, but was necessitated by the limited number of recordings available for many males. However, analyses of songs of individual Alder Flycatchers (Lovell and Lein 2004), Willow Flycatchers (*E. traillii*) (MRL, unpubl. data), and Dusky Flycatchers (*E. oberholseri*) (Stehelin 2005) demonstrate little variation among recordings across the breeding season. They also show that patterns of variability within and among individuals are similar when comparisons are made using either single recordings of individuals or multiple recordings made on different dates.

Analysis Using Spectrographic Cross Correlation.—Spectrographic cross correlation (SPCC) was conducted using the CORMAT routine in SIGNAL 4.0. Similarity values calculated by CORMAT are somewhat sensitive to the exact parameters used to generate spectrograms because of the trade-off between time resolution and frequency resolution inherent in the Fast Fourier Transform procedure. Preliminary analyses indicated that spectrograms with a Hanning window (WINDOW = HANN), 64-point transforms (XFTLEN = 64), and 500 steps (XFTSTP = 500) provided maximum similarity values. These produced "wide-band" spectrograms with time and frequency resolutions of 3.2 ms and 312.5 Hz, respectively. Use of a fixed number of steps is justified because CORMAT adds zero-amplitude segments to short signals to bring all component signals to the length of the longest signal. However, because of the different durations of the two types of songs, transform intervals and overlaps varied slightly between song types (0.45 ms and 86% for Type 1 songs, 0.54 ms and 83% for Type 2 songs).

CORMAT produces a lower triangular half-matrix in which each value is the peak cross correlation value for a pair of signals. Values for comparisons of a signal with itself and reciprocal comparisons between each pair of signals are omitted. SPCC of 184 signals resulted in a half-matrix of 16,836 ($n(n - 1)/2$) comparisons of different pairs of songs of each type. I wrote a Fortran program to calculate mean values for the 28 comparisons among the eight songs sampled from each male (within-male similarity) and the 64 comparisons of songs between each pair of males (between-male similarity), creating a 23×23 triangular half-matrix for each song type. Mean similarity values in these two matrices were averaged to create a third matrix containing a mean index of similarity for each male-male comparison.

Normal parametric tests could not be used to evaluate differences between within-male and between-male similarity values because the similarity values in the matrices were not independent observations (each song of each male was used in multiple comparisons). Randomization tests (Manly 1997) using Resampling Stats software (Blank et al. 2001) and 1,000 iterations tested whether the difference between mean within-male and mean between-male similarity values in each matrix was greater than expected by chance.

I divided the between-male similarity values into those involving comparisons within a single range and those involving comparisons between ranges to examine differences in songs between the two mountain ranges. I tested for significant differences between within-range and between-range similarity values using Mantel tests (Sokal and Rohlf 1995). Similarity values were converted to dissimilarity values by subtracting each from 1. The half-matrices of dissimilarity values were compared with a design half-matrix containing a 0 in each cell representing a within-range comparison and a 1 in each cell representing a between-range comparison.

Analysis Using Multivariate Comparisons.—A series of temporal and frequency variables was measured or calculated for the same songs used in the SPCC analysis (8 examples of each song type for each of 23 individuals). A representative sample of songs was examined to ascertain which temporal

TABLE 1. Time and frequency variables measured or calculated from audiospectrograms of Type 1 and Type 2 songs of Buff-breasted Flycatchers. Variables indicated with * were measured only for Type 1 songs.

Code	Variable (units)
DURN	Duration of entire song (ms)
PK1T	Duration from start of song of first frequency "peak" (ms)
PK2T	Duration from start of song of second frequency "peak" (ms)
PK3T*	Duration from start of song of third frequency "peak" (ms)
VALT	Duration from start of song of frequency "valley" (ms)
STRF	Frequency at start of song (Hz)
ENDF	Frequency at end of song (Hz)
PK1F	Maximum frequency at first frequency "peak" (Hz)
PK2F	Maximum frequency at second frequency "peak" (Hz)
PK3F*	Maximum frequency at third frequency "peak" (Hz)
VALF	Minimum frequency at frequency "valley" (Hz)
P2VFR	Frequency difference between first frequency peak and frequency valley (Hz)
P1P2FR	Frequency difference between first and second frequency peaks (Hz)
P1PN	Relative time of first frequency peak (PK1T ÷ DURN)
P2PN	Relative time of second frequency peak (PK2T ÷ DURN)
P3PN*	Relative time of third frequency peak (PK3T ÷ DURN)
VPN	Relative time of frequency valley (VALT ÷ DURN)

and frequency characteristics could be measured with objectivity and were repeatable prior to final measurements. Sound in both song types is modulated up and down in frequency repeatedly, producing a series of "peaks" and "valleys" on the spectrogram. The first peak is identical between song types for each individual. Type 1 songs have one more modulation than Type 2 songs resulting in one additional peak and valley. The final set of variables measured included the duration of the song, and the times and frequencies of the peaks (3 for Type 1 songs, 2 for Type 2 songs) and valleys. No measurements were made for the first valley in Type 1 songs because some individuals exhibited a break in sound production at this point with no clear inflection in frequency.

Temporal and frequency measurements were made in a semi-automated fashion using custom programs written in the SIGNAL command language. Points were measured on a spectral contour generated from the spectrogram. The spectral contour tracks the frequency with the maximum sound energy at a given time. Sound amplitude increases gradually at the start of songs and fades out gradually at the end, and the apparent locations of these points can be shifted on spectrograms by modifying the parameters controlling spectrogram intensity. Consequently, start and end times of the song were defined arbitrarily as the points at which the spectral contour exceeded (start) or fell below (end) an amplitude threshold of 20 dB below the maximum amplitude of the spectrogram. This procedure resulted in a consistent approximation of these times because the amplitude of all songs was normalized prior to analysis. Frequencies at the start and end of the song were extracted from the spectral contour at these times. Similarly, times of peaks and valleys were defined as the points of local maxima (peaks) or minima (valleys) of frequency in the spectral contour. Five temporal and six frequency variables were measured for Type 1 songs (Table 1). Only four temporal and five frequency variables were measured for Type 2 songs because these songs have one fewer frequency peak. Additional variables (6 for Type 1 songs, 5 for Type 2 songs) were calculated from the measured variables (Table 1).

I calculated coefficients of variation (CV) for each variable for each song type to quantify the magnitude of variability. I calculated within-male coefficients of variation (CV_w) to measure variation within a single recording and among-male coefficients of variation (CV_a) from the variable means from each male. A one-way ANOVA was conducted on each variable to compare within-male and among-male variation.

I conducted principal components analyses (PCA) on the data sets for each song type be-

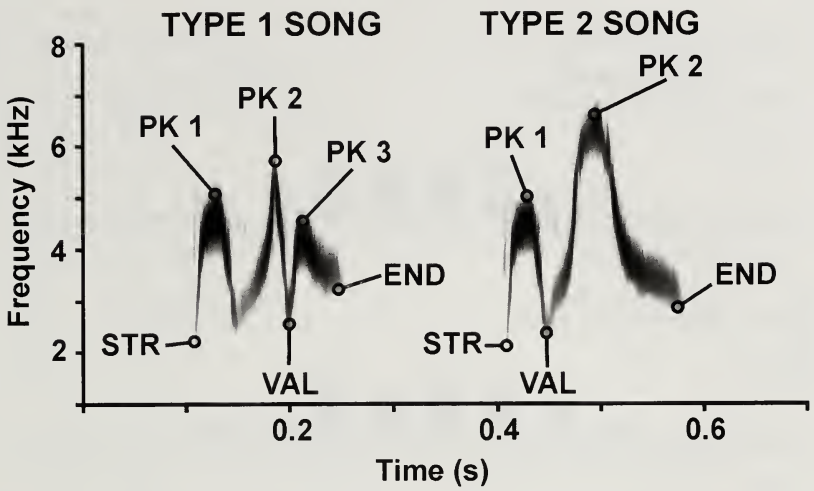


FIG. 2. Audiospectograms of Type 1 and Type 2 songs of Buff-breasted Flycatchers indicating the reference points for temporal and frequency measurements (STR = Start; PK = Peak; VAL = Valley).

cause some of the variables were highly correlated with one another. This produced a smaller number of uncorrelated variables (PC scores) for each song, which were entered into a discriminant function analysis (DFA) to examine whether songs of different individuals could be distinguished. Results of jack-knifed classifications, in which each song was assigned to an individual using discriminant functions calculated from all songs in the data set except the one being classified, are reported as percentages of songs assigned correctly. This is a conservative estimate of the power of the classification procedure (Manly 1994).

I conducted a similar analysis to test whether songs of individuals from the two mountain ranges could be reliably distinguished. This analysis used mean values of variables for the eight songs of each type for each individual to maintain sample independence.

SYSTAT 10.2 was used for parametric statistical analyses. Probability plots were used to check variables for an approximate fit to a normal distribution before parametric statistical tests were applied. I report mean values ± SD and use a criterion of $\alpha < 0.05$ for statistical significance.

RESULTS

Visual examination of spectrograms revealed small differences between songs of different individuals (Fig. 1). These differences were reflected in the time and frequency variables measured (Fig. 2), and were consistent from song to song within a single recording and across recordings made over the course of a season (M. R. Lein, unpubl. data). However, these differences are not detectable by ear in the field or on recordings.

Mean similarity values between pairs of songs, calculated using SPCC (Table 2), were significantly higher for comparisons of songs within individuals than for comparisons between individual males for Type 1 songs (randomization test, $P < 0.001$), Type 2 songs (randomization test, $P < 0.001$), and average

TABLE 2. Similarity values calculated by spectrographic cross correlation for comparison of songs within and between individual Buff-breasted Flycatchers.

	Mean similarity value ± SD (Range)	
	Within-male comparisons (n = 23)	Between-male comparisons (n = 253)
Song Type 1	0.88 ± 0.03 (0.84–0.93)	0.65 ± 0.10 (0.38–0.86)
Song Type 2	0.84 ± 0.04 (0.79–0.93)	0.57 ± 0.10 (0.33–0.79)
Average	0.86 ± 0.02 (0.82–0.91)	0.61 ± 0.08 (0.36–0.81)

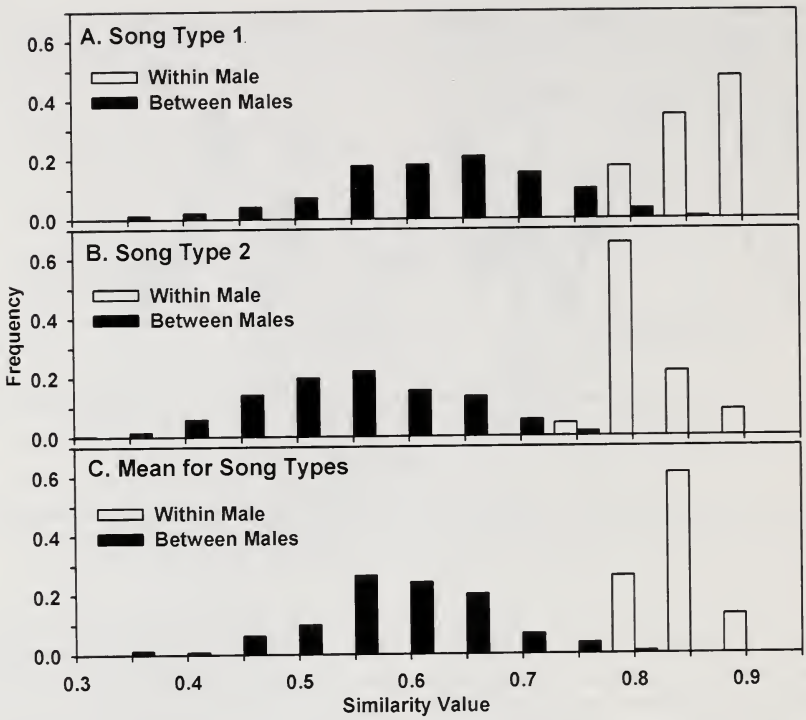


FIG. 3. Similarity values from spectrographic cross correlation of different songs from individual male Buff-breasted Flycatchers (within-male) or of songs from different pairs of males (between-male). A. Song Type 1. B. Song Type 2. C. Average for song types.

similarity values (randomization test, $P < 0.001$). Both within-male and between-male values had considerable variation (Table 2, Fig. 3) with minor overlap in the ranges for both Type 1 and Type 2 songs. However, when similarity values for the two song types were averaged for each comparison (i.e., for each individual male or for each pair of males), there was no overlap in the ranges (Table 2). The maximum average similarity value for between-male comparisons was 0.81 while the minimum value for within-male comparisons was 0.82.

There were no significant differences in similarity values for comparisons between males within a single mountain range and comparisons between males from different mountain ranges (Table 3) for Type 1 songs (Mantel test, $g = 0.714$, $P = 0.20$), Type 2 songs ($g = -0.271$, $P = 0.45$) or average similarity values ($g = 0.295$, $P = 0.34$). The ranges of similarity values for the two types of comparisons overlapped completely (Fig. 4).

Univariate analyses indicated that all variables measured or calculated for individual songs of both types varied significantly more among individuals than within individuals (Tables 4, 5; one-way ANOVAs, all $P <$

TABLE 3. Similarity values calculated by spectrographic cross correlation for comparison of songs between individual Buff-breasted Flycatchers within the same mountain range (either Chiricahua Mountains or Huachuca Mountains) and between mountain ranges.

	Mean similarity value ± SD (Range)	
	Within-range comparisons (n = 123)	Between-range comparisons (n = 130)
Song Type 1	0.65 ± 0.10 (0.38–0.86)	0.64 ± 0.10 (0.39–0.84)
Song Type 2	0.57 ± 0.10 (0.36–0.78)	0.57 ± 0.10 (0.33–0.79)
Average	0.61 ± 0.08 (0.39–0.80)	0.61 ± 0.08 (0.36–0.81)

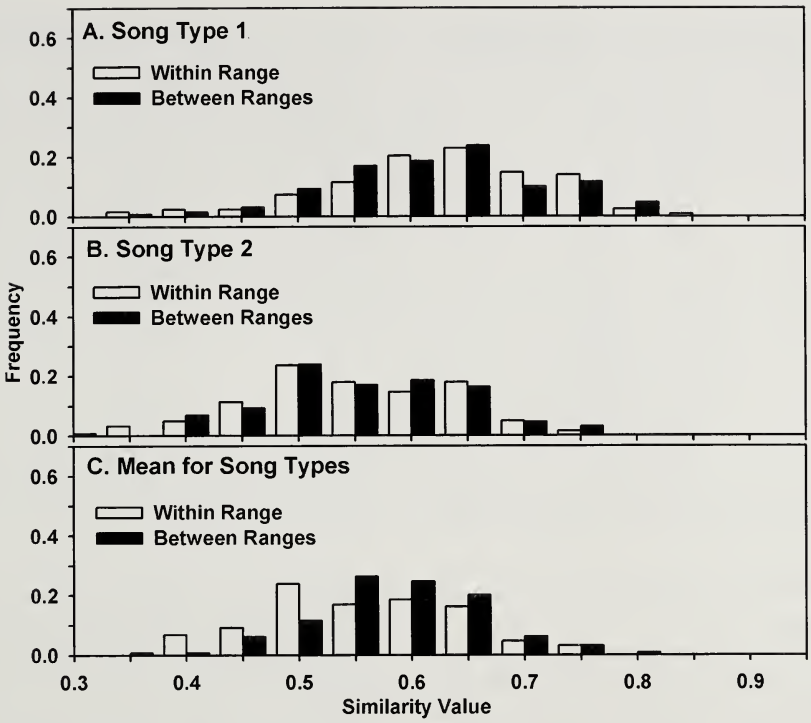


FIG 4. Similarity values from spectrographic cross correlations of songs of pairs of male Buff-breasted Flycatchers from the same mountain range (within-range) or from different mountain ranges (between-range). A. Song Type 1. B. Song Type 2. C. Average for song types.

TABLE 4. Descriptive statistics and coefficients of variation for 17 variables measured or calculated for eight Type 1 songs for each of 23 male Buff-breasted Flycatchers.

Variable	Mean ± SD	Mean CV_w (Range)	CV_a	$F_{22, 161}$[a]
DURN	150.6 ± 11.4	3.0 (1.4–5.5)	7.6	40.0
PK1T	16.7 ± 2.9	11.9 (6.1–20.1)	17.2	9.4
PK2T	81.2 ± 6.7	2.7 (0.9–5.3)	8.3	57.1
PK3T	107.4 ± 7.0	2.8 (1.1–4.7)	6.5	34.9
VALT	94.7 ± 6.7	2.5 (1.2–4.0)	7.1	54.0
STRF	2825.4 ± 374.4	9.3 (3.3–16.6)	13.3	7.1
ENDF	3383.9 ± 267.8	3.1 (1.0–6.9)	7.9	40.4
PK1F	4469.7 ± 172.0	1.0 (0.4–2.3)	3.8	96.6
PK2F	5292.7 ± 288.1	1.3 (0.2–2.8)	5.4	112.9
PK3F	4089.8 ± 166.8	1.2 (0.3–2.5)	4.1	74.3
VALF	2548.5 ± 264.9	2.0 (0.8–3.9)	10.4	187.6
P2VFR	2744.3 ± 371.0	2.7 (0.9–4.1)	13.5	179.9
P1P2FR	823.0 ± 265.8	10.6 (3.2–20.2)	32.3	70.0
P1PN	11.1 ± 2.0	11.7 (5.0–21.4)	18.0	12.1
P2PN	54.0 ± 3.8	2.6 (0.9–4.3)	7.0	47.0
P3PN	71.5 ± 4.5	3.0 (1.0–5.6)	6.2	24.7
VPN	63.0 ± 4.3	2.6 (1.3–4.0)	6.8	43.5

[a] *F*-values for ANOVAs comparing within- and among-male variation for each variable; all $P < 0.001$.

TABLE 5. Descriptive statistics and coefficients of variation for 14 variables measured or calculated for eight Type 2 songs for each of 23 male Buff-breasted Flycatchers.

Variable	Mean ± SD	Mean CV_w (Range)	CV_a	$F_{22, 161}$[a]
DURN	193.2 ± 15.1	2.3 (0.9–3.6)	7.8	78.2
PK1T	18.8 ± 2.7	8.2 (2.9–16.3)	14.3	12.0
PK2T	93.5 ± 7.4	3.7 (1.8–5.4)	8.0	28.5
VALT	37.8 ± 4.9	3.7 (0.9–7.9)	12.8	65.5
STRF	2288.0 ± 236.9	3.8 (1.4–7.9)	10.4	44.1
ENDF	2912.3 ± 292.6	3.6 (1.4–6.8)	10.0	48.0
PK1F	4463.6 ± 168.3	0.8 (0.4–1.9)	3.8	151.5
PK2F	6871.2 ± 390.3	1.4 (0.3–3.2)	5.7	93.8
VALF	2691.8 ± 203.3	3.1 (0.9–6.4)	7.6	32.0
P2VFR	4179.4 ± 379.0	3.2 (1.5–6.3)	9.1	49.8
P1P2FR	2407.6 ± 333.5	4.4 (0.9–9.0)	13.9	54.8
P1PN	9.8 ± 21.5	8.6 (4.0–28.3)	15.7	15.4
P2PN	48.6 ± 4.7	4.0 (2.5–6.1)	9.6	38.6
VPN	19.7 ± 3.0	4.2 (1.5–6.9)	15.4	86.9

[a] *F*-values for ANOVAs comparing within- and among-male variation for each variable; all $P < 0.001$.

0.001). The ratio of CV_a/mean CV_w was >1 for all variables.

PCA of the variables generated 5 principal components (PCs) with eigenvalues >1.0 explaining 85.3% of the variation in the original variables for Type 1 songs, and 5 PCs with eigenvalues >1.0, explaining 81.9% of the variation in the original variables for Type 2 songs. MANOVAs on the scores of individual songs on the five PCs, conducted as part of DFA, indicated highly significant differences among multivariate means for different individuals for both Type 1 songs ($F_{110,773} = 54.5$, $P < 0.001$) and Type 2 songs ($F_{110,773} = 56.3$, $P < 0.001$). Jack-knifed classifications assigned 156 of 184 Type 1 (84.8%) and 159 of 184 Type 2 songs (86.4%) to the correct individual.

Univariate analyses of variables averaged over the eight songs of each type for each individual indicated three frequency variables measured or calculated for Type 1 songs differed significantly between males from the Chiricahua and Huachuca mountains (Table 6). There was no difference between mountain ranges in other variables for Type 1 songs (all $F_{1,21} \leq 2.4$, all $P \geq 0.137$) or in any variable for Type 2 songs (all $F_{1,21} \leq 2.9$, all $P \geq 0.101$).

PCA of the individual means for the variables generated 5 PCs with eigenvalues >1.0 for each song type explaining 87.4 and 85.6% of the variation in the original variables for Type 1 and Type 2 songs, respectively. MANOVAs on the scores for individual males on the five PCs indicated no significant differences in multivariate means between the two mountain ranges for either Type 1 ($F_{5,17} = 2.1$, $P = 0.115$) or Type 2 songs ($F_{5,17} = 1.1$, $P = 0.419$). Jack-knifed classifications assigned 14 of 23 individuals (60.9%) to the correct mountain range in DFAs for each song type. This does not differ ($\chi^2 = 0.91$, $P = 0.34$) from the frequency expected if individuals were assigned randomly to mountain ranges.

DISCUSSION

Both analyses indicate that both song types of Buff-breasted Flycatchers are individually

TABLE 6. Variables measured or calculated for Type 1 songs of Buff-breasted Flycatchers that showed significant differences between birds from the Chiricahua Mountains and the Huachuca Mountains, Arizona.

	Mean ± SD (Hz)			
Variable	Chiricahua Mtns (n = 13)	Huachuca Mtns (n = 10)	$F_{1,21}$	P
ENDF	3508.0 ± 70.2	3222.6 ± 133.0	10.4	0.004
VALF	2649.1 ± 253.9	2417.7 ± 228.3	5.1	0.034
P2VFR	2612.8 ± 411.7	2915.1 ± 229.7	4.3	0.050

distinctive. SPCC showed almost no overlap in similarity values for within-male and between-male comparisons (Fig. 3), while DFA showed a high level of accuracy in assignment of songs to the correct individual. Most measured or calculated variables showed little variation within individuals (CV_w values <5%, Tables 4, 5). Many different features of songs had high CV_a/mean CV_w ratios (Tables 4, 5) indicating their potential to differentiate among individuals (Robisson et al. 1993, Bee et al. 2001, Vignal et al. 2004).

The "errors" in classification of songs in the DFA are also instructive. Nineteen of 28 Type 1 songs assigned to an incorrect individual were associated with "reciprocal errors" in which one song of male A was assigned to male B and one song of male B was assigned to male A. Many of the misclassifications were also consistent with the findings of the SPCC analysis. For example, DFA assigned five Type 1 songs of male SPRG (from Sawmill Canyon in the Huachuca Mountains) to male SNAG (from West Turkey Creek in the Chiricahua Mountains), and three Type 1 songs of SNAG to SPRG. This pair had an extremely high between-male similarity value (0.84), indicating the close similarity of their Type 1 songs despite their geographical separation. Examination of the results for Type 2 songs showed similar patterns.

Both techniques failed to demonstrate significant differences in songs of males between the two mountain ranges. There was no separation of between-male similarity values calculated for comparisons within a single mountain range from those for comparisons between ranges (Fig. 4). Three of 31 variables showed significant univariate differences between the two ranges (Table 6). This did not result in a correct classification of songs by DFA that was significantly better than expected by chance. This finding demonstrates the potential danger of basing analyses of song variation on a small number of variables that are often chosen subjectively. Selected variables may not accurately reflect overall patterns of variation.

The absence of differentiation in songs between the two mountain ranges is also apparent from examination of the SPCC results for pairs of males with between-male similarity values that approach those typical of within-male comparisons. Six of the nine between-male similarity values >0.8 for Type 1 songs, and four of six between-male similarity values >0.75 for Type 2 songs, were for comparisons between males from different ranges. There appears to be no relation between song similarity of pairs of males and geographic proximity.

It is reassuring that both analytical techniques produced qualitatively similar results. However, they approach the question of variation differently and, therefore, each is best suited to address different kinds of questions. SPCC is rapid, but provides only a single value for similarity between each pair of songs. It provides no information about the ways in which the two songs are similar or different from each other. Multivariate analysis of a large set of temporal and frequency measurements is time consuming, and has an element of subjectivity in choosing appropriate features for measurement. However, it does permit identification of the acoustic features in which different samples of songs differ.

It has been suggested that DFA may be used to assign individual identities to "unknown" recordings (Terry et al. 2001). Discriminant functions generated from songs of known reference individuals are used to classify the unknown songs. These songs will be assigned to the correct individuals if there is sufficient information in the song features used in the DFA. However, this technique has a serious potential drawback. It is poorly-suited to handle "true unknowns", that is, songs of "new" individuals that are not included in the sample of reference individuals used to generate the discriminant functions. DFA forces assignment of all songs to one of the pre-existing categories (individuals).

SPCC does not have this drawback. "Unknown" songs from an individual in the reference sample will be identified correctly. They will have high similarity values with known songs from that individual, and relatively low similarity values with other individuals in the reference sample. Songs of a "true unknown" will have low similarity values with all males in the reference sample and may be identified as coming from a "new" individual.

SPCC does have a serious potential problem that must be recognized. It works best for

relatively simple sounds without silent intervals separating different elements. If two songs had identical elements, but differed in the timing of the intervals separating them, the elements would show progressively less temporal overlap during the duration of the songs. This would result in a low cross correlation value even though the sound elements were identical (Khanna et al. 1997). This problem is probable with songs more complex than those of *Empidonax* flycatchers. However, it is possible to divide complex songs into a series of elements, to conduct SPCCs on the different elements (Nelson et al. 1995), and to combine or average the cross correlation values for the different elements of two songs into a single measure of similarity. This would parallel the procedure used to generate an average similarity value across the two song types of Buff-breasted Flycatchers.

ACKNOWLEDGMENTS

Valerie Haines provided able assistance in the field and made many of the original recordings. Stephen Russell, Josiah and Valere Austin, and Sheridan Stone provided valuable advice or logistical support for the field work. Tara Stehelin acquired the digital sound files from the recordings. Critical comments from Valerie Haines, Sarah Hechtenthal, and Scott Lovell greatly improved the final manuscript. Field work was conducted under permits from the USDA–Coronado National Forest and the U.S. Army–Fort Huachuca Military Reservation. The research was evaluated and approved by the Life and Environmental Sciences Animal Care Committee of the University of Calgary (Protocol 96-006) and was supported by a grant from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

American Ornithologists' Union (AOU). 1998. Check-list of North American birds. Seventh Edition. American Ornithologists' Union, Washington, D.C., USA.

Baker, M. C. and D. M. Logue. 2003. Population differentiation in a complex bird sound: a comparison of three bioacoustical analysis procedures. Ethology 109:223–242.

Baptista, L. F. and J. R. King. 1980. Geographical variation in song and song dialects of montane White-crowned Sparrows. Condor 82:267–284.

Bee, M. A., C. E. Kozich, K. J. Blackwell, and H. C. Gerhardt. 2001. Individual variation in advertisement calls of territorial male green frogs, *Rana clamitans*: implications for individual discrimination. Ethology 107:65–84.

Blank, S., C. Seiter, and P. Bruce. 2001. Resampling Stats add-in for Excel user's guide. Resampling Stats Inc., Arlington, Virginia, USA.

Borror, D. J. 1960. The analysis of animal sounds. Pages 26–37 *in* Animal sounds and communication (W. E. Lanyon and W. N. Tavolga, Editors). American Institute of Biological Sciences, Washington, D.C., USA.

Bowers Jr., R. K. and J. B. Dunning Jr. 1994. Buff-breasted Flycatcher (*Empidonax fulvifrons*). The birds of North America. Number 125.

Clark, C. W., P. Marler, and K. Beeman. 1987. Quantitative analysis of animal vocal phonology: an application to Swamp Sparrow song. Ethology 76:101–115.

Johnson, N. K. 1963. Biosystematics of sibling species of flycatchers in the *Empidonax hammondi-oberholseri-wrightii* complex. University of California Publications in Zoology 66:79–238.

Johnson, N. K. 1980. Character variation and evolution of sibling species in the *Empidonax difficilis-flavescens* complex (Aves: Tyrannidae). University of California Publications in Zoology 112:1–153.

Khanna, H., S. L. L. Gaunt, and D. A. McCallum. 1997. Digital spectrographic cross-correlation: tests of sensitivity. Bioacoustics 7:209–234.

Kroodsma, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24.

Kroodsma, D. E. 1996. Ecology of passerine song development. Pages 3–19 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Editors). Cornell University Press, Ithaca, New York, USA.

Lanyon, W. E. 1978. Revision of the *Myiarchus* flycatchers of South America. Bulletin of the American Museum of Natural History 161:427–628.

Lovell, S. F. and M. R. Lein. 2004. Song variation in a population of Alder Flycatchers. Journal of Field Ornithology. 75:146–151.

Manly, B. J. F. 1994. Multivariate statistical methods: a primer. Second Edition. Chapman and Hall, London, United Kingdom.

Manly, B. J. F. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Second Edition. Chapman and Hall, London, United Kingdom.

Martin, J. A. 1997. Distribution, abundance, and habitat characteristics of the Buff-breasted Flycatcher in Arizona. Thesis. University of Arizona, Tucson, USA.

Nelson, D. A., P. Marler, and A. Palleroni. 1995. A comparative approach to vocal learning: intraspecific variation in the learning process. Animal Behaviour 50:83–97.

Payne, R. B. and P. Budde. 1979. Song differences and map distances in a population of Acadian Flycatchers. Wilson Bulletin 91:29–41.

Robisson, P., T. Aubin, and J.-C. Brémond. 1993. Individuality in the voice of the Emperor Penguin *Aptenodytes forsteri*: adaptation to a noisy environment. Ethology 94:279–290.

Sedgwick, J. A. 2001. Geographic variation in the song of Willow Flycatchers: differentiation between *Empidonax traillii adastus* and *E. t. extimus*. Auk 118:366–379.

Smith, W. J. 1969. Displays of *Sayornis phoebe* (Aves, Tyrannidae). Behaviour 33:283–322.

Smith, W. J. 1970. Song-like displays in *Sayornis* species. Behaviour 37:64–84.

Smith, W. J. 1988. Patterned daytime singing of the Eastern Wood-Pewee, *Contopus virens*. Animal Behaviour 36:1111–1123.

Sokol, R. R. and F. J. Rohlf. 1995. Biometry. Third Edition. W. H. Freeman and Company, New York, USA.

Stehelin, T. E. 2005. Variation in syllable structure and singing behaviour in a population of Dusky Flycatchers (*Empidonax oberholseri*). Thesis. University of Calgary, Calgary, Alberta, Canada.

Stein, R. C. 1963. Isolating mechanisms between populations of Traill's Flycatcher. Proceedings of the American Philosophical Society 107:21–50.

Terry, A. M. R., P. K. McGregor, and T. M. Peake. 2001. A comparison of some techniques used to assess vocal individuality. Bioacoustics 11:169–188.

Vignal, C., N. Mathevon, and S. Mottin. 2004. Audience drives male songbird response to partner's song. Nature 430:448–451.

Wiley, R. H. 2005. Individuality in songs of Acadian Flycatchers and recognition of neighbours. Animal Behaviour 70:237–247.

The Wilson Journal of Ornithology 120(2):268–276, 2008

PHYLOGENETIC RELATIONSHIP AND SONG DIFFERENCES BETWEEN CLOSELY RELATED BUSH WARBLERS (*CETTIA SEEBOHMI* AND *C. DIPHONE*)

SHOJI HAMAO,[1,5] MARIA J. S. VELUZ,[2] TAKEMA SAITOH,[3] AND ISAO NISHIUMI[4]

ABSTRACT.—We investigated the phylogenetic relationship and differences in the song structure between the Philippine Bush Warbler (*Cettia seebohmi*) and the Japanese Bush Warbler (*C. diphone*). We compared complete sequences of the mitochondrial cyt-b gene of *C. seebohmi* to those of other *Cettia* taxa from GenBank and found *C. seebohmi* formed a monophyletic group with *C. haddeni* and *C. diphone*. The phylogenetic tree also suggests that *C. seebohmi* is more closely related to *C. haddeni* than to *C. diphone* although this was not strongly supported due to the low bootstrap values. The estimated nucleotide differences between *C. seebohmi* and *C. haddeni* (4.37%), and between *C. seebohmi* and *C. diphone* (3.87–4.37%) were larger than the intersubspecific difference between *C. diphone borealis* and *C. d. cantans* (2.44%). *Cettia seebohmi*, *C. haddeni*, and *C. diphone* diverged prior to the subspecies divergences of *C. diphone*. The basic structure of songs was similar in *C. seebohmi* and *C. diphone*; all songs consisted of pure monotone whistles followed by variably modulated warbles. However, sonagraphic parameters showed statistically significant differences between species. It is reasonable to regard *C. seebohmi* and *C. diphone* as separate species. *Received 26 February 2007. Accepted 8 September 2007.*

Bush Warblers (*Cettia* spp.) radiated in southeast Asia and the southwest Pacific, although one species, *C. cetti* (Cetti's Warbler), is distributed in Europe. Molecular phylogenetics suggest the southwestern Pacific species (i.e., *C. ruficapilla* on the Fiji Islands, *C. annae* on the western Caroline Islands, *C. parens* on the southern Solomon Islands, and *C. haddeni* on the northern Solomon Islands) are monophyletic, and the continental *C. diphone* (Japanese Bush Warbler) belongs to a different clade from these island forms (Lecroy and Barker 2006). That study, however, did not include *C. seebohmi* (Philippine Bush Warbler), which is distributed between the island and continental forms.

Cettia seebohmi is similar to *C. diphone* in morphology and plumage, although slight differences occur in plumage color (Delacour 1942, Kennedy et al. 2000), wing shape, and male body size (Hamao et al. 2006a). It is endemic to northwestern Luzon, Philippines (Grant 1894, Kennedy et al. 2000), while *C. diphone* breeds in eastern China, southern Ussuriland, Korea, and Japan (Ornithological Society of Japan 2000). These two Bush Warblers are considered different species (Grant 1894, Dickinson et al. 1991, Kennedy et al. 2000), although some authors consider both as *C. diphone* (Delacour 1942, Baker 1997). The Ornithological Society of Japan (2000) also describes the breeding range of *C. diphone* as including the Philippines, indicating the two Bush Warblers are regarded as the same species. Thus, it is important to investigate the genetic relationship between *C. seebohmi* and *C. diphone* to understand the taxonomy of these closely related forms and the evolution of *Cettia* in southeast Asia and the southwest Pacific.

Differences in song structure between related species contribute to reproductive isolation between them, because vocalization is a recognition cue between species (de Kort et al. 2002, Matyjasiak 2005). Birds can avoid heterospecific matings by discriminating between songs of conspecifics and heterospecifics. Therefore, differences in song structure between *C. seebohmi* and *C. diphone* are useful for understanding their evolutionary rela-

[1] Institute for Nature Study, National Museum of Nature and Science, 5-21-5 Shiroganedai, Minato-ku, Tokyo, 108-0071 Japan.

[2] Zoology Division, National Museum of the Philippines, P. Burgos Street, Manila, 1000, Philippines.

[3] Department of Life Sciences, Rikkyo University, 3-34-1 Nishi-Ikebukuro, Toshima-ku, Tokyo, 171-8501 Japan.

[4] Department of Zoology, National Museum of Nature and Science, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo, 169-0073 Japan.

[5] Corresponding author; e-mail: hamao@kahaku.go.jp

tionship. Our objectives are to show: (1) the phylogenetic relationship and divergence time between *C. seebohmi* and *C. diphone* using mitochondrial DNA sequences, and (2) differences in the acoustic structure of their songs.

METHODS

Study Sites and Fieldwork.—The study site for *C. seebohmi* was an open forest with dense bush at Ambangeg (16° 31′ N, 120° 50′ E; 1,355 m elevation) in the Cordillera Mountains of northwestern Luzon, Philippines. We recorded songs of 20 males on 26–27 April 2005 and collected 20–30-μL blood samples by brachial venipuncture from two males and a female for DNA analysis.

The study sites for *C. diphone* were deciduous secondary forests that included patches of previously cultivated but presently abandoned lands dominated by dwarf bamboo (*Pleioblastus chino*) in Saitama, central Honshu, Japan: one at Furusato (36° 06′ N, 139° 18′ E; 70 m elevation) and the other at Shogunsawa (36° 01′ N, 139° 20′ E; 50 m elevation). We recorded songs of 38 males; 16 males at Furusato on 16 June 2003, and 5 and 17 males at Shogunsawa on 26 May and 2 June 2003, respectively.

We recorded each singing male for at least 3 min using a Sony TCD-D8 DAT recorder with a Sony ECM-G3M directional microphone. Each recording was sufficient to record all song types of the male because the repertoires were small and the birds sang frequently (reported for *C. diphone* by Hamao 1992, 1993; Momose 1999).

Sequence Analysis.—DNA was extracted from blood samples using standard phenol/chloroform extraction. Polymerase chain reaction (PCR) amplifications of entire mitochondrial cytochrome b (cyt-b) gene and partial NADH dehydrogenase subunit V (ND5) were performed using primers (H = heavy strand; L = light strand; numbers give the position of the 3′-end in the *Gallus gallus* mitochondrial genome): mt-F (H-16065), 5′-GGA GTC TTC AGT TTT TGG TTT ACA AGA C-3′ (Helbig and Seibold 1999) and L14080ND5P, 5′-TCA ACY CAY GCM TTC TTC AAA GC-3′ (modified from Sorenson et al. 1999). These two primers gave an approximately 2.0-kb product. Primers mt-F and L14764ND5HCZ, 5′-TGA TTT AAR CTM MTA GGA CCA GAA GG-3′ (Nishiumi and Kim 2004) were used for sequencing.

PCR was performed in volumes of 10 μL containing 10 ng of total genomic DNA, 0.2 mM of each dNTP, 1.5 mM $MgCl_2$, 0.4 μM of each primer, and 0.2 units of Taq DNA polymerase (Takara Ex-taq). Amplifications were performed using a Takara PCR Thermal Cycler MP (Takara) under the following conditions: 30 sec at 94° C, 30 sec at 52° C, and 90 sec at 72° C (35 cycles). Samples were incubated at 94° C for 3 min before the cyclic reactions and, after completion, at 72° C for 5 min. We placed 2 μL of the reaction product on a 1.5% agarose gel in 0.5 × TBE buffer to check the success of the reaction. The remainder of the PCR product was purified using ExoSAP-IT (Amersham Bioscience, Piscataway, NJ, USA).

PCR products were sequenced with the BigDye Terminator Cycle Sequencing v3.1 Cycle sequencing Kit (Applied Biosystems, Foster, CA, USA) on an ABI PRISM™ 3100-Avant (Applied Biosystems, Foster, CA, USA). Sequencing reactions were performed in volumes of 10 μL containing 50 ng of PCR product, 1.5 μL of Terminator Ready Reaction Mix, 1.25 μL of 5 × Sequencing Buffer, and 1.6 pmol of the sequencing primer. The reactions were conducted under the following conditions using a Takara PCR Thermal Cycler MP: 10 sec at 96° C, 5 sec at 50° C, and 4 min at 60° C (25 cycles). Samples were incubated at 96° C for 1 min before the cyclic reactions. Products were purified using ethanol/EDTA/sodium acetate precipitation according to the sequencing kit manual.

Genetic and Phylogenetic Analyses.—We compared complete sequences of the mitochondrial cyt-b gene of three individuals of *C. seebohmi* to those of four other *Cettia* taxa from GenBank (*C. diphone borealis* from Korea: AB159198; *C. d. cantans* from Japan and Korea: AB159194-AB159197; *C. haddeni* from the northern Solomon Islands: DQ066451; *C. fortipes* from Taiwan: L77122), which are all of the *Cettia* species that had complete cyt-b sequences available from GenBank. We used three other species from GenBank (*Urosphena squameiceps* [Asian Stubtail]: AB159177, AB159179; *Sylvia atricapilla* [Eurasian Blackcap]: Z73494; *Acrocephalus orientalis* [Oriental Reed War-

bler]: AB159186) as an outgroup for the phylogenetic analysis.

Sequences were aligned by eye with ATGC v4.0.8 and Genetix-Mac v10.1 (Genetix). An appropriate substitution model for the data set was estimated via the Akaike information criterion (AIC; Akaike 1974) and a hierarchical likelihood ratio test (Posada and Crandall 1998), both calculated in MODELTEST 3.7 (Posada and Crandall 1998). The choice of cyt-b model was based on the best-fit model according to the AIC. The sequences of *Cettia* and *Urosphena* were included in the product data set. The selected model for cyt-b was a transversional model (Posada and Crandall 1998) with a gamma distribution (TVM + G; settings: empirical base frequencies of π_A = 0.2814, π_C = 0.3570, π_G = 0.1233, π_T = 0.2382, transition/transversion ratio = 7.7216, gamma distribution shape parameter α = 0.1037). Phylogenetic trees were constructed using different approaches: neighbor joining (NJ; Saitou and Nei 1987), maximum parsimony and maximum likelihood (MP and ML; PAUP v4.0b1 from Swofford 2003), and Bayesian inference of phylogeny (MrBAYES 3.1.2; Huelsenbeck and Ronquist 2001). The robustness of clades was estimated by 1,000 bootstrap replicates in NJ and MP (Felsenstein 1985), 100 bootstrap replicates in ML, and by Bayesian posterior probabilities in Bayesian inference using Markov chain Monte Carlo (MCMC). Four Metropolis-coupled MCMC chains with incremental heating temperature 0.1 were run for 1,000,000 generations and sampled every 100 generations. Two analyses were run simultaneously starting from random trees. The first 25% of generations were discarded as "burn-in" and the posterior probability was estimated for the remaining generations. Samples from the stationary phases of the independent runs were pooled to obtain the final results.

The nucleotide divergence between populations is shown as the Kimura two-parameter distance (%) calculated by MEGA v.3.1 (Kumar et al. 2004). We used 1.6% per million years (MY) and 2.0% per MY of the cyt-b substitution rates for small birds to estimate divergence time (Fleischer et al. 1998, and Moore and DeFilippis 1997, respectively).

Song Analysis.—All recorded sounds were analyzed with computer software (SAS-Lab Pro. Version 4.2, Raimund Specht). Sounds were displayed as sonagrams. FFT-lengths of 256 and 1024 were used to produce plots of temporal and frequency measures, respectively. Songs of both the Philippine and Japanese Bush warblers consisted of an initial constant frequency (CF) part and a subsequent frequency modulated (FM) part (Momose 1999). We measured nine sonagraphic parameters of each song type, which represented song structure (Fig. 1): CF part, (1) frequency, (2) number of notes; FM part, (3) maximum frequency, (4) minimum frequency, (5) frequency range, (6) duration, (7) number of notes, (8) number of frequency inflections, i.e., number of changes in the sign of the derivative (slope) of the frequency in the sonagram, and (9) modulation rate, i.e., number of frequency inflections/sec. We also measured the number of song types of each male, as males used a small number of stable song types (reported for *C. diphone* by Momose 1999, Hamao and Ueda 2000).

We performed Mann-Whitney *U*-tests with a sequential Bonferroni correction (Rice 1989) to assess the table-wide type I error rate when comparing song parameters between the two species. We used the average values for individual males and considered them independent data points.

RESULTS

Phylogenetic Relationships and Genetic Distances.—Complete mitochondrial cyt-b sequences from three individuals of *C. seebohmi* were obtained and deposited in GenBank (accessions AB281094-6). They were compared to the sequences available in GenBank of *C. haddeni*, *C. fortipes*, and two subspecies of *C. diphone*.

Phylogenetic analysis showed *C. seebohmi* formed a monophyletic group with *C. haddeni* and *C. diphone* (the bootstrap values were 69, 100, 69, and 100 by NJ, MP, ML, and Bayes, respectively) (Fig. 2). All four different models inferred that *C. seebohmi* is more closely related to *C. haddeni* than to *C. diphone*, although the monophyly of *C. seebohmi* and *C. haddeni* was not strongly supported (the bootstrap values were 76, 63, 56, and 56 by NJ, MP, ML, and Bayes, respectively).

The estimated nucleotide difference between *C. seebohmi* and *C. diphone borealis*

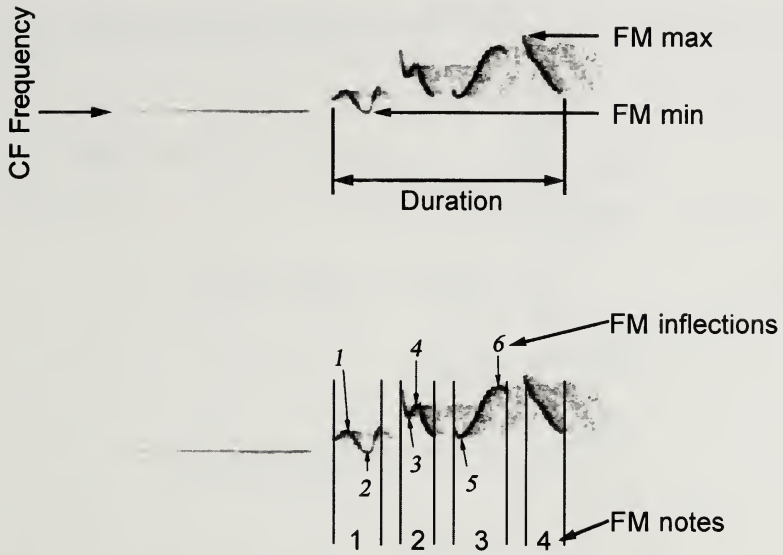


FIG. 1. Parameters used for song structure measurements of *Cettia seebohmi* and *C. diphone*. Constant frequency (CF frequency), frequency modulated maximum (FM max), minimum frequency (FM min), duration, number of frequency inflections (FM inflections), and number of notes (FM notes).

(3.87%) was smallest among those between the species (Table 1). However, the difference between *C. seebohmi* and *C. diphone cantans* (4.37%) was equivalent to that between *C. seebohmi* and *C. haddeni*. These differences were larger than the inter-subspecific difference in *C. diphone* (2.44%).

The divergence time of *C. seebohmi* from *C. diphone borealis* was estimated to be 1.94–2.42 million years ago (MYA), which is older than between subspecies *C. d. borealis* and *C. d. cantans* (1.22–1.53 MYA), but equivalent to that between *C. seebohmi* and *C. haddeni* or *C. diphone cantans* (2.19–2.73 MYA) (Table 2).

Song Structure.—A male *C. seebohmi* (male #2) had four song types (Fig. 3). The songs consisted of pure monotone whistles (CF parts) followed by variably modulated warbles (FM parts), except for one song type lacking the CF part (Fig. 3). A male *C. diphone* (male #34) also had four song types, and the CF and FM parts in the songs (Fig. 3). The basic structure of songs was similar in other males of both species.

All sonagraphic parameters had statistically significant differences between species (Table 3). The number of notes in CF parts was larger in *C. diphone* than in *C. seebohmi*. The frequency was higher in the songs of *C. seebohmi* than in *C. diphone* in both the CF and FM parts. The frequency range of FM parts was wider in *C. seebohmi* than in *C. diphone*. The FM parts of *C. seebohmi* had a longer duration, and more notes and inflections, although the modulation rate was lower. Individual males of *C. seebohmi* had fewer song types than those of *C. diphone*. Thus, songs of *C. seebohmi* had higher frequency and a wider frequency range, and were more complexly modulated than those of *C. diphone*. However, males of *C. seebohmi* had less variable songs.

DISCUSSION

Genetic distance seemingly suggests that *C. seebohmi* is most closely related to *C. diphone borealis* (Table 1). However, the distance between *C. seebohmi* and the other subspecies of *C. diphone* (i.e., *C. d. cantans*) was equivalent to that between *C. seebohmi* and *C. haddeni*. Therefore, from the results of genetic distances, it is equivocal which species, *C. diphone* or *C. haddeni*, is more closely related to *C. seebohmi*. The molecular phylogenetic tree suggests that *C. seebohmi* is more closely related to *C. haddeni* than to *C. diphone*, but this was not strongly supported due to the low bootstrap values (Fig. 2). Thus, further examination is needed to identify the phylogenetic position of *C. seebohmi*.

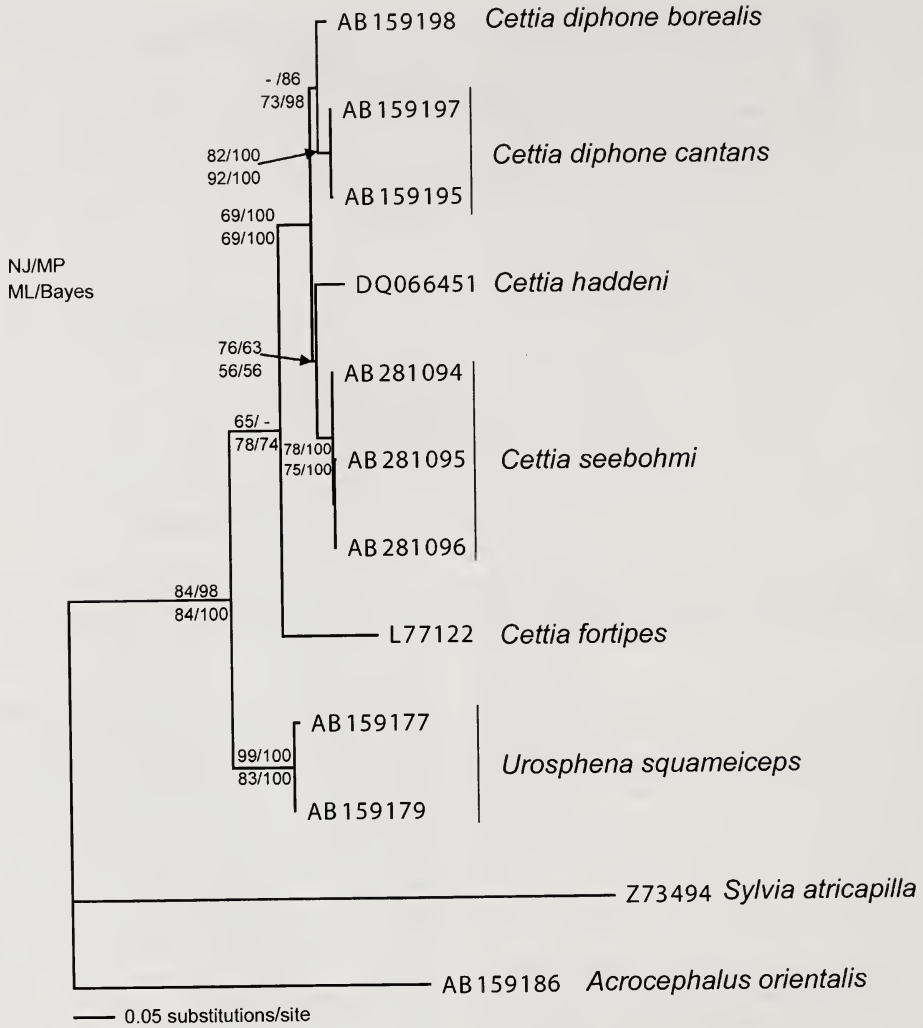


FIG. 2. Neighbor-joining tree of cyt-b sequences from *Cettia* and *Urosphena*. The tree was rooted using *Sylvia atricapilla* and *Acrocephalus orientalis* as outgroups. Numbers at each terminal are GenBank accessions; numbers at each node indicate bootstrap support (above, neighbor joining/maximum parsimony; below, maximum likelihood/Bayes).

TABLE 1. Kimura two-parameter distances (%) between *Cettia* spp. in southeast Asia and the southwest Pacific.

	Taxonomic unit	1	2	3	4	5	6
1	*Cettia diphone borealis*						
2	*Cettia diphone cantans*	2.44					
3	*Cettia haddeni*	4.74	5.24				
4	*Cettia seebohmi*	3.87	4.37	4.37			
5	*Cettia fortipes*	10.60	10.11	13.04	11.17		
6	*Urosphena squameiceps*	9.91	10.40	11.57	9.90	11.77	

TABLE 2. Estimated divergence time (MYA) between *Cettia* spp. in southeast Asia and the southwest Pacific under the assumption of 1.6 and 2.0%/MY substitution rates.

	Taxonomic unit	1	2	3	4
1	*Cettia diphone borealis*				
2	*Cettia diphone cantans*	1.22–1.53			
3	*Cettia haddeni*	2.37–2.96	2.62–3.28		
4	*Cettia seebohmi*	1.94–2.42	2.19–2.73	2.19–2.73	

The estimation of divergence time suggests that *C. seebohmi* and *C. haddeni* diverged 2.19–2.73 MYA, and that *C. seebohmi* and *C. diphone* diverged 1.94–2.73 MYA. This suggests that *Cettia* species in southeast Asia and the southwest Pacific radiated at nearly the same time, at the end of the Pliocene. Monarch flycatchers (Family Monarchidae) diversified across the Pacific archipelagos in a single radiation (Filardi and Moyle 2005). Evolution of *Cettia* species shows a similar pattern, indicating that in some avian taxa, this is a common pattern when birds radiate on Pacific islands.

The estimated nucleotide difference between the Korean and Japanese subspecies of *C. diphone* (*borealis* and *cantans*, respectively) was 2.44%, which is similar to that estimated by Kajita (2002): 2.3% difference in the cyt-b gene between Japanese subspecies (i.e., *C. d. cantans* [throughout Japan], *C. d. diphone* [Bonin Islands], and *C. d. restricta* [Minami-Daito Island, extinct but recovered on Okinawa Island by Kajita et al. 2002]), and the continental subspecies (i.e., *C. d. borealis* [Korea] and *C. d. canturians* [China]). The divergence time of *C. d. borealis* with *C. d. cantans* was estimated to be 1.22-1.53 MYA. These results suggest the continental ancestor of *C. diphone* dispersed to the main and peripheral islands in Japan, and formed subspecies in the Pleistocene.

The songs of both *C. seebohmi* and *C. diphone* consist of CF and FM parts (Fig. 3). This basic song structure was also found in other *Cettia* species (i.e., *C. fortipes* in Taiwan [Wells 1982, Orenstein and Pratt 1983, Rozendaal 1987], *C. carolinae* in the Tanimbar Islands [Rozendaal 1987], *C. ruficapilla* in the Fiji Islands [Orenstein and Pratt 1983], and *C. annae* in the Caroline Islands [Orenstein and Pratt 1983]). The similarity in song structure may be caused by the similar habitats of the species. The initial CF part in songs of *C. di-*

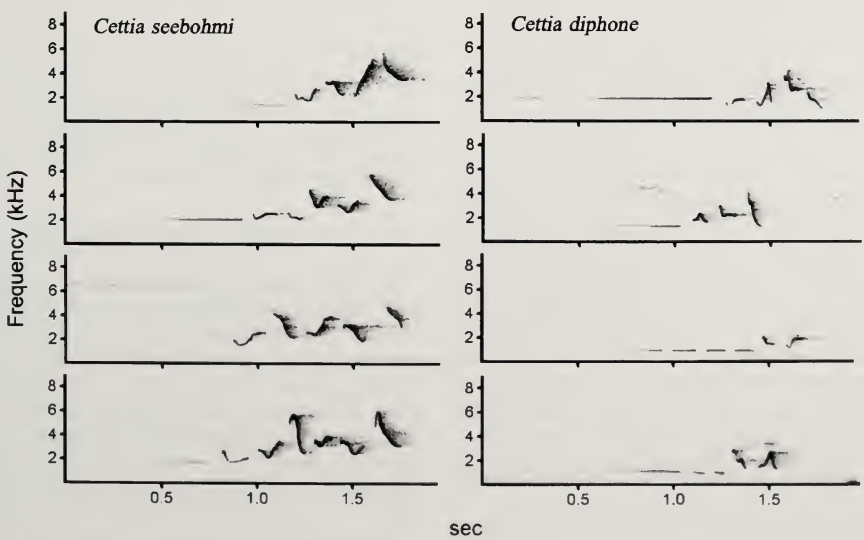


FIG. 3. Basic song structure of *Cettia seebohmi* (left) and *C. diphone* (right). Four song types of one male are shown for each species.

TABLE 3. Song features (means ± SD) of *Cettia seebohmi* and *C. diphone*. Numbers in parentheses are number of males.

	C. seebohmi (20)	*C. diphone* (38)	*P*
Song structure			
CF frequency (kHz)	1.67 ± 0.10	1.25 ± 0.15	<0.001*
CF notes	1.00 ± 0.00	2.70 ± 0.52	**
FM max (kHz)	5.79 ± 0.23	3.35 ± 0.36	<0.001*
FM min (kHz)	1.62 ± 0.12	1.25 ± 0.11	<0.001*
FM width (kHz)	4.12 ± 0.27	2.10 ± 0.39	<0.001*
FM duration (sec)	0.81 ± 0.10	0.30 ± 0.06	<0.001*
FM notes	5.2 ± 0.5	2.9 ± 0.5	<0.001*
FM inflections	8.6 ± 1.3	3.9 ± 1.2	<0.001*
FM modulation rate	10.56 ± 1.51	12.82 ± 3.77	<0.01*
Repertoire size			
No. of song types	2.3 ± 0.8	3.0 ± 0.9	<0.01*

* *U*-test with Bonferroni correction.
** *U*-test was not performed because of the large difference in the variances between the species.

phone may be an adaptation to a bushy environment (Momose 1986). The habitats of both *C. seebohmi* and *C. diphone* are roughly the same: thickets, shrubs, and forest undergrowth (Kennedy et al. 2000, Ornithological Society of Japan 2000) in which pure monotonal whistles may have high carrying ability (Morton 1975).

The sonagraphic parameters of songs differed between *C. seebohmi* and *C. diphone* (Table 3). The frequency was higher in *C. seebohmi* that had smaller body size than *C. diphone* (Hamao et al. 2006a). Smaller birds produce songs with higher frequencies (Ryan and Brenowitz 1985), which may affect the difference in frequency. The other possible factor related to these differences is vegetation density. The habitat of *C. diphone* is dense bamboo thickets and shrubs at the forest edge and forest floor (Nakamura and Nakamura 1995, Ornithological Society of Japan 2000), while the habitat of *C. seebohmi* is thickets and the understory of open forests (Kennedy et al. 2000). The songs of *C. seebohmi* had a higher frequency, a wider frequency range, and a more complex modulation pattern. These vocalization features are connected to open habitats (e.g., Hunter and Krebs 1979, Shy 1983, Anderson and Conner 1985) due to sound transmission properties of the habitats (Morton 1975).

Cettia diphone males did not show statistically significant differences in their responses to *C. seebohmi* and *C. diphone* songs in a song playback experiment (Hamao et al. 2006b), but this does not directly indicate they are the same species. Males may lose their territory and paternity if they regard conspecific rivals as heterospecifics. In contrast, if females regard heterospecific males as conspecifics, they may suffer a greater cost by producing hybrid offspring. There is a difference in the cost of misidentifying potential competitors and mates. Therefore, males and females should differ in species recognition (Searcy and Brenowitz 1988). Variable songs are more likely to be acceptable for males.

Cettia seebohmi diverged from *C. haddeni* and *C. diphone* prior to the subspecies divergences of *C. diphone*. Its songs have the same basic structure as those of *C. diphone*, but apparently differ in sonagraphic parameters. It is reasonable to regard *C. seebohmi* and *C. diphone* as separate species.

ACKNOWLEDGMENTS

We thank the Department of Environment and Natural Resources (DENR), Parks and Wildlife Bureau (PAWB), and the DENR–CAR (Cordillera Administrative Region) for permits and logistical support. We especially thank Teber Dionisio, Yolly Ruperto, and Emerita Tamiray of Mt. Pulag. We also thank Hiroyuki Morioka and Manabu Kajita for assistance with the literature search, and Francis Veluz and Nicky Icarangal for field assistance. This study was planned as one of the "Natural History Researches of the Island Arcs in the Western Pacific" by the National Museum of Nature and Science, Tokyo, and was partly supported by the Japan Ministry of Education, Culture,

Sports, Science, and Technology (grant 17770076 to IN). Finally, we thank three anonymous reviewers and C. E. Braun for improving the manuscript.

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Anderson, M. J. and R. N. Conner. 1985. Northern Cardinal song in three forest habitats in eastern Texas. Wilson Bulletin 97:436–449.

Baker, K. 1997. Warblers of Europe, Asia and Northern Africa. Helm identification guides. Christopher Helm Publishers, London, United Kingdom.

de Kort, S. R., P. M. Den Hartog, and C. Ten Cate. 2002. Diverge or merge? The effect of sympatric occurrence on the territorial vocalizations of the Vinaceous Dove *Streptopelia vinacea* and the Ring-necked Dove *S. capicola*. Journal of Avian Biology 33:150–158.

Delacour, C. J. 1942. The Bush Warblers of the genera *Cettia* and *Bradypterus*, with notes on allied genera and species. Ibis 84:509–519.

Dickinson, E. C., R. S. Kennedy, and K. C. Parkes. 1991. The birds of the Philippines, an annotated check-list. British Ornithologists' Union, Oxford, United Kingdom.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

Filardi, C. E. and R. G. Moyle. 2005. Single origin of a pan-Pacific bird group and upstream colonization of Australasia. Nature 438:216–219.

Fleischer, R. C., C. E. Mcintosh, and C. L. Tarr. 1998. Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. Molecular Ecology 7:533–545.

Grant, W. R. O. 1894. On the birds of the Philippine Islands. Part II. The highlands of north Luzon, 5000 feet. Ibis (6th Series) 6:501–522.

Hamao, S. 1992. Lack of pair-bond: a polygynous mating system of the Japanese Bush Warbler *Cettia diphone*. Japanese Journal of Ornithology 40: 51–65.

Hamao, S. 1993. Individual identification of male Japanese Bush Warblers *Cettia diphone* by song. Japanese Journal of Ornithology 41:1–7.

Hamao, S. and K. Ueda. 2000. Simplified song in an island population of the Bush Warbler *Cettia diphone*. Journal of Ethology 18:53–57.

Hamao, S., M. J. S. Veluz, and I. Nishiumi. 2006a. Difference in morphology between two closely related Bush Warblers, *Cettia diphone* and *C. seebohmi*, in Japan and the Philippines. Miscellaneous Reports of the Institute for Nature Study 37: 17–26.

Hamao, S., M. J. S. Veluz, and I. Nishiumi. 2006b. Species recognition by song between the Luzon Bush Warbler, *Cettia seebohmi*, and the Japanese Bush Warbler, *C. diphone*. Memoirs of the National Science Museum 44:21–29.

Helbig, A. J. and I. Seibold. 1999. Molecular phylogeny of Palearctic-African *Acrocephalus* and *Hippolais* warblers (Aves: Sylviidae). Molecular Phylogenetics and Evolution 11:246–260.

Huelsenbeck, J. P. and F. R. Ronquist. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

Hunter, M. L. and J. R. Krebs. 1979. Geographical variation in the song of the Great Tit, *Parus major*, in relation to ecological factors. Journal of Animal Ecology 48:759–785.

Kajita, M. 2002. Within-species phylogeny and biogeography in *Cettia diphone*. Iden 56:42–46.

Kajita, M., T. Mano, and F. Sato. 2002. Two forms of Bush Warbler *Cettia diphone* occur on Okinawajima Island: re-evaluation of *C. d. riukiuensis* and *C. d. restricta* by multivariate analyses. Journal of Yamashina Institute for Ornithology 33: 148–167.

Kennedy, R. S., P. C. Gonzales, E. C. Dickinson, H. C. Miranda Jr., and T. H. Fisher. 2000. A guide to the birds of the Philippines. Oxford University Press, Oxford, United Kingdom.

Kumar, S., K. Tamura, and M. Nei. 2004. MEGA3: Integrated software for molecular evolutionary genetics analysis and sequence alignment. Briefings in Bioinformatics 5:150–163.

Lecroy, M. and F. K. Barker. 2006. A new species of Bush-warbler from Bougainville Island and a monophyletic origin for southwest Pacific *Cettia*. American Museum Novitates 3511:1–20.

Matyjasiak, P. 2005. Birds associate species-specific acoustic and visual cues: recognition of heterospecific rivals by male Blackcaps. Behavioral Ecology 16:467–471.

Momose, H. 1986. Mechanism of maintaining territories by acoustic communication. Pages 127–157 *in* Reproductive strategies of birds (S. Yamagishi, Editor). Toukaidaigaku-shuppankai, Tokyo, Japan.

Momose, H. 1999. Structure of territorial songs in the Japanese Bush Warbler (*Cettia diphone*). Memoirs of the Faculty of Science, Kyoto University (Series Biology) 16:55–65.

Moore, W. S. and V. R. deFilippis. 1997. The window of taxonomic resolution for phylogenies based on mitochondrial cytochrome b. Pages 83–113 *in* Avian molecular evolution and systematics (D. P. Mindel, Editor). Academic Press, San Diego, California, USA.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. American Naturalist 109:17–34.

Nakamura, T. and M. Nakamura. 1995. Birds' life in Japan with color pictures: birds of mountain, woodland and field. Hoikusya, Osaka, Japan.

Nishiumi, I. and C.-H. Kim. 2004. Little genetic differences between Korean and Japanese populations in songbirds. National Science Museum Monographs 24:279–286.

Orenstein, R. I. and H. D. Pratt. 1983. The relation-

ships and evolution of the southwest Pacific warbler genera *Vitia* and *Psamathia* (Sylviinae). Wilson Bulletin 95:184–198.

Ornithological Society of Japan. 2000. Check-list of Japanese birds. Sixth and Revised Edition. Ornithological Society of Japan, Obihiro, Japan.

Posada, D. and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Rozendaal, F. G. 1987. Description of a new species of Bush Warbler of the genus *Cettia* Bonaparte, 1834 (Aves: Sylviidae) from Yamdena, Tanimber Islands, Indonesia. Zoologische Mededelingen 61: 177–202.

Ryan, M. J. and E. A. Brenowitz. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist 126: 87–100.

Saitou, N. and M. Nei. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 4: 406–425.

Searcy, W. A. and E. A. Brenowitz. 1988. Sexual differences in species recognition of avian song. Nature 332:152–154.

Shy, E. 1983. The relation of geographical variation in song to habitat characteristics and body size in North American tanagers (Thraupinae: *Piranga*). Behavioral Ecology and Sociobiology 12:71–76.

Sorenson, M. D., J. C. Ast, D. E. Dimcheff, T. Yuri, and D. P. Mindell. 1999. Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. Molecular Phylogenetics and Evolution 12:105–114.

Swofford, D. L. 2003. Phylogenetic analysis using parsimony (and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts, USA.

Wells, D. R. 1982. Biological species limits in the *Cettia fortipes* complex. Bulletin of the British Ornithologists' Club 102:57–62.

The Wilson Journal of Ornithology 120(2):277–285, 2008

AUTUMN STOPOVER NEAR THE GULF OF HONDURAS BY NEARCTIC-NEOTROPIC MIGRANTS

ANDREW B. JOHNSON[1,2,3] AND KEVIN WINKER[1]

ABSTRACT.—The southeastern Yucatan Peninsula hosts high numbers of transient Nearctic-Neotropic migrants during autumn migration, but the importance of this region during migratory stopover has not been addressed. We studied autumn stopover body mass gains among passerine migrants in tropical lowland forest 20 km inland from the Gulf of Honduras. Most individuals captured had some subcutaneous fat. Ten of 15 taxa with sufficient sample sizes had significant positive diel (24 hr) gains in a body condition index. Estimates of net mass gains in these 10 taxa suggested they all were depositing fat; average individuals in four of these taxa were depositing sufficient fuel to undertake an entire night of migration after only 1 day of fattening: *Empidonax* spp., Red-eyed Vireo (*Vireo olivaceus*), Gray Catbird (*Dumetella carolinensis*), and Northern Waterthrush (*Seiurus noveboracensis*). Two (Wood Thrush [*Hylocichla mustelina*] and Common Yellowthroat [*Geothlypis trichas*]) of the four species apparently not gaining mass at the study site migrate late in the season and occurred only after Hurricane Iris severely altered the habitat. Four other species (Gray Catbird, Magnolia Warbler [*Dendroica magnolia*], American Redstart [*Setophaga ruticilla*], and Indigo Bunting [*Passerina cyanea*]) had significant gains in mass after the hurricane. These data demonstrate the importance of the region as an autumn stopover site for some species and suggest that stopover areas farther north are also important to migrants passing through the southeastern part of the Yucatan Peninsula. *Received 19 January 2006. Accepted 25 September 2007.*

The geography of North America causes Nearctic-Neotropic migrants that breed across thousands of square kilometers of boreal and temperate forest to funnel through a small fraction of the land area in the forests of Central America during the nonbreeding season. This concentration of migrants likely makes forests in Central America vital as both wintering and stopover habitat. Many migrant species have winter ranges that extend far beyond the Gulf of Honduras (AOU 1998), and forests adjacent to the Gulf of Honduras are probably important stopover habitat. Published accounts of high volumes of transient Nearctic-Neotropic migrants in Panama (Galindo et al. 1963, Galindo and Mendez 1965) suggest there should be similar numbers of migrants farther north. Monroe (1968) documented a large spring migration northward across the Gulf of Honduras and speculated that a large autumn migration also occurs. However, there has been no information published about how transient migrants use stopover sites in this region.

Few studies have addressed energetic needs of migrants in Central America (Rogers and Odum 1966; Child 1969; Winker 1995a, b), and there are no published studies of migrant stopover ecology near the Gulf of Honduras. We chose a site near the Gulf of Honduras in lowland tropical forest to examine the autumn migration of Nearctic-Neotropic migrants. We provide the first extensive data on autumn stopover by woodland migrants in this region and address the following questions: (1) what levels of fat are carried in the region; (2) do migrants refuel at this site and, if so, to what extent; and (3) do species that have farther to migrate fuel more?

METHODS

Study Area.—Our study site was a 25-year-old, second-growth, lowland forest adjacent to a citrus orchard in the floodplain of the Rio Grande (16° 16′ N, 88° 52′ W) near Big Falls Village, Toledo District, Belize (Fig. 1). The site was in a matrix of human-altered habitats (primary forest remnants, citrus orchard, fields, and habitats in stages of regrowth) that had a canopy height of ~20 m with some gaps filled with dense woody vegetation and vine tangles 3 m in height.

Trapping.—We established a 1.26-ha study site in August 2001 and placed 30 12-m mist nets in two parallel rows of 15 nets spaced 30 m apart. Each net was spaced 30 m apart from its neighbor within each row, and we alter-

[1] University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775, USA.

[2] Current address: Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87131, USA.

[3] Corresponding author; e-mail: ajohnson@unm.edu

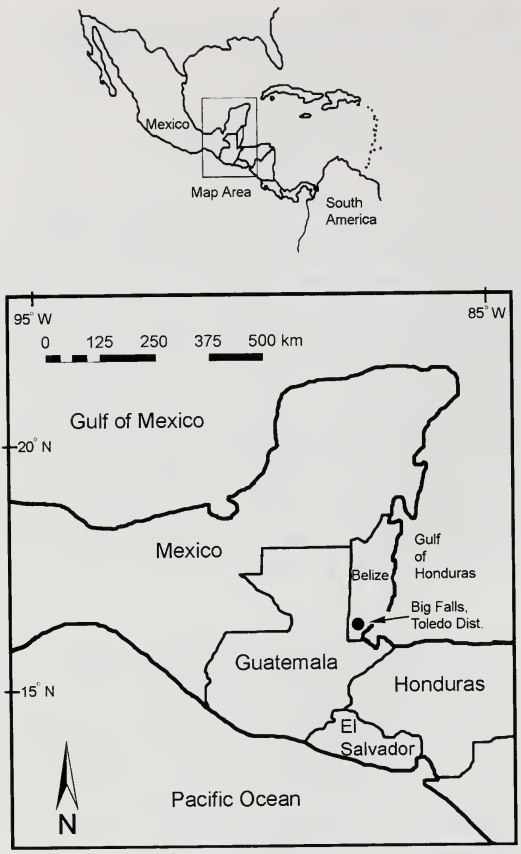


FIG. 1. Big Falls, Toledo District study site in Belize in northern Central America on the Yucatan Peninsula.

nated mesh sizes between 30 and 36 mm. Nets were opened beginning on 11 August and were open all day when conditions permitted. We accrued 8,805 net hrs until 7 October, when we removed nets from the study site in anticipation of Hurricane Iris, which struck on 8 October. The effect of Hurricane Iris on the site changed the habitat from a nearly closed, 20-m high canopy to a 5-m high tangle of uprooted and broken trees, broken branches, and vines. We re-opened 15 nets placed on the original site on 19 October. Five nets were placed in their original net lanes and others were placed as close as possible to their original positions. Placement of nets was constrained by the drastically altered forest structure (e.g., fallen trees and dense tangles of vines). We only netted during mornings and evenings during this period due to lack of shade on the site. We accrued 1,114 more net hrs and concluded the effort on 15 November.

Each bird captured was identified to species, age class, and whether it was male or female when possible. Time and net of capture, body mass, and chord of closed wing (hence 'wing chord,' as traditionally used, see Stiles and Altshuler 2004) were recorded for all birds captured; tail, tarsometatarsus, and bill lengths were recorded for most individuals. Subcutaneous fat deposits were scored following Helms and Drury (1960). All *Empidonax* were treated as a single taxon for this study, and included five Nearctic-Neotropic migrant species verified by museum specimens (*traillii*, *alnorum*, *flaviventris*, *virescens*, and *minimus*).

Daily Mass Gains.—The extent of mass gain was estimated at the species level following Winker et al. (1992) and Winker (1995a). This method calculates a condition index for each individual and examines the relationship between condition index and time of capture using simple linear regression.

Rising and Somers (1989) and Freeman and Jackson (1990) suggested that no single linear external measurement of a bird is a good correlate of body size, although these studies suggested that tarsometatarsus ("tarsus") or tibiotarsus was the best univariate indicator of body size. However, Connell et al. (1960) and Rogers and Odum (1964, 1966) showed that wing length was a good predictor of fat-free mass in some passerines during migration, although they did not examine other variables. Winker (1995a) found a condition index based on wing chord or tail to be a better predictor of fat content than one based on tarsus in a sample of fat-extracted Tennessee Warblers (*Vermivora peregrina*). We used wing chord to standardize body mass by calculating a condition index for all species except Kentucky Warbler (*Oporornis formosus*).

A condition index for each individual was calculated by dividing its mass by its wing chord (Winker 1995a). The condition index was examined for each species with respect to time of day (equivalent to time of capture of each individual; hereafter referred to simply as 'time') using simple linear regression. Regressions of fat scores, mass, and condition indices using other morphological characters (tail, tarsometatarsus, and bill lengths) with

respect to time were used to corroborate wing chord condition index trends. A condition index constructed using the first principal component of wing chord, tail length, tarsometatarsus, and bill lengths combined was also explored as an option, but the estimates were not an improvement over the use of a single morphological character. Multiple regression was also tried (Dunn 2000), but the estimates were similar and did not justify the added complexity of the analyses.

Estimates of net 24-hr mass changes were made for species having regression slopes of condition index with respect to time significantly different from zero ($\alpha = 0.05$). The slope of the condition index regression was converted to estimated daily gross mass gains for the average individual in a species by multiplying by 12.42 hrs (average length of daily bird activity from field notes) and multiplying by the sample's mean wing chord. Net mass gains were calculated by subtracting estimates of nightly metabolic demands from the estimated gross daily gains. Our estimate of nocturnal loss was a mass-specific existence metabolism estimate (Kendeigh 1970:60) using both fat-free mass data when available (Dunning 1993) and average "lean mass" (Dunn 2002) from birds captured at the site.

We used a value of 30.2 kJ energy per g fuel (Pennycuick 2003) for our flight capacity estimates, which assumes the fuel used during migration is 95% fat. Our taxon-averaged flight capacity estimates would have to be revised downward from our present energetic estimates if it is found that migrants in this region are depositing protein to the extent as trans-Sahara Eurasian Blackcaps (*Sylvia atricapilla*) (Karasov and Pinshow 1998). Fuel composed of 30% protein would reduce our flight capacity estimates by about 50% (Pennycuick 2003: equation 12).

We assumed mass gain was not the result of rehydration after migration (Nisbet et al. 1963). Catabolism of lipids produces water that helps to maintain water balance, and Rogers and Odum (1966) showed that, even in emaciated post-flight birds in Panama, water content was not different from that of fat birds. Bauchinger and Biebach (2000) also showed that water content did not differ among pre-migratory, immediately post-migratory, or post-migratory birds that had 7 days to recover with free access to food and water.

Morphological data for each taxon were checked for normality. Mass and morphological variables used to estimate net mass gains in each species were normally distributed except for wing chord in American Redstart (*Setophaga ruticilla*). Transformations of wing chord for American Redstart failed to normalize these data. Tail length was not recorded in this species. Residuals were checked for normality using quantile-quantile plots following regression analyses and examined visually to ascertain whether there were any patterns that indicated unequal variance. Residuals were normal and no patterns indicating heteroscedasticity were found in any of these taxa.

Hurricane Iris struck on 8 October 2001 and the drastic habitat change that resulted may have had an effect on fat deposition by migrants. No taxon had sufficiently large sample sizes ($n \geq 30$) pre- and post-hurricane to conduct separate analyses before and after the storm. Consequently, each migrant taxon was based on a sample from either entirely before or entirely after the hurricane; samples were not pooled between pre- and post-hurricane efforts.

Flight Capacity Estimates.—Maximum hours of flight possible for the average individual gain in each taxon at the site were calculated using net gain estimates from this study, published values for the energetic content of fuel (30.2 kJ per g; Pennycuick 2003), and size-specific rate of energy use during migration (Tucker 1974). These values were used to estimate the duration an average individual of each species could fly in a night. The methodology of Pennycuick (1989) was not applicable because we did not record wing span measurements.

Mass Comparisons.—Condition index analyses provide a species-level estimate of daily gains in mass, but do not consider the amount of fat already carried by individuals of a species. Average mass from each species was compared to its fat-free mass to examine the fat load the average individual of each species was carrying (Dunning 1993), and to average "lean mass" (mean mass of individuals from our site with fat scores of zero; Dunn 2002) using two-sample *t*-tests. The paucity of in-

dividuals of some species that had fat scores of zero at our site made the latter comparison tenuous (e.g., no Red-eyed Vireos [*Vireo olivaceus*] or Veeries [*Catharus fuscescens*] had fat scores of zero).

RESULTS

We captured 30 or more individuals of 14 species and the genus *Empidonax*, and present summary statistics of morphological characters to allow comparisons with other studies (Table 1). We encountered no emaciated individuals. We rarely observed actively growing feathers and assumed that energetic demands for the vast majority of these birds were limited to migration and maintenance costs.

Comparisons of Mass with Fat-free and Lean Mass.—All taxa but Wood Thrush (*Hylocichla mustelina*) were significantly heavier than the species' average fat-free mass (Table 2), and most individuals were carrying visible subcutaneous fat (82% of the individuals of the 15 taxa had fat scores >0). Many Veeries and Swainson's Thrushes (*Catharus ustulatus*) had heavy fat loads (Table 1; all Veeries had fat scores >0). Few taxa were significantly heavier than lean mass, but all taxa except Wood Thrush were significantly heavier than fat-free mass (Table 2). We observed frequent defecation by birds during handling that suggested they were feeding at this site. The peak of migration, especially of *Catharus* thrushes, corresponded with ripening of large amounts of fruits on our site, particularly the understory tree, *Dendropanax arboreus* (Araliaceae).

Estimates of Daily Mass Gain.—Eleven taxa had significant slopes of mass with respect to time (Table 3). Nine taxa had regressions of wing chord condition index with respect to time with significant *F*-values (slopes different from zero); all slopes were positive (Table 3). Kentucky Warblers and Veeries did not show significant gains in wing chord condition index, even though regressions of mass on time had significant positive slopes, and fat score regressions with respect to time also showed significant positive slopes for Kentucky Warblers (Table 3). Both species had marginal *P*-values for gain in wing chord condition index with respect to time (Kentucky Warbler, $P = 0.064$; Veery, $P = 0.068$).

Four taxa had significantly positive slopes

TABLE 1. Mean ± SD morphological characters (*n*) of autumn migrants mist-netted at Big Falls, Belize, 11 August–15 November 2001.

Species	Mass	Wing chord	Tail length	Tarsus[a] length	Fat score
Empidonax spp.	11.73 ± 1.39 (88)	65.88 ± 3.14 (88)	54.19 ± 2.93 (86)	15.52 ± 0.98 (88)	0.7 (79)
Red-eyed Vireo, *Vireo olivaceus*	16.88 ± 1.50 (39)	74.92 ± 2.35 (39)	50.44 ± 2.97 (39)	17.67 ± 1.32 (39)	1.3 (39)
Veery, *Catharus fuscescens*	32.15 ± 4.29 (67)	92.70 ± 3.05 (67)	66.51 ± 3.75 (67)	28.85 ± 1.46 (67)	1.7 (67)
Swainson's Thrush, *C. ustulatus*	29.36 ± 3.13 (305)	93.22 ± 2.90 (305)	64.05 ± 3.25 (305)	26.99 ± 1.39 (305)	1.7 (305)
Wood Thrush[b], *Hylocichla mustelina*	42.93 ± 3.17 (45)	101.36 ± 3.69 (45)	68.00 ± 2.54 (19)	30.01 ± 0.99 (19)	0.7 (42)
Gray Catbird[b], *Dumetella carolinensis*	34.35 ± 2.88 (268)	85.53 ± 2.44 (269)	88.02 ± 4.29 (117)	Not measured	1.4 (265)
Magnolia Warbler[b], *Dendroica magnolia*	7.17 ± 0.47 (78)	56.46 ± 2.26 (77)	47.70 ± 2.19 (76)	17.24 ± 0.93 (5)	0.6 (79)
American Redstart[b], *Setophaga ruticilla*	6.93 ± 0.50 (34)	57.71 ± 1.84 (31)	53.71 ± 2.13 (28)	16.76 ± 0.59 (27)	0.4 (34)
Worm-eating Warbler, *Helmitheros vermivorus*	12.27 ± 0.80 (31)	64.85 ± 1.86 (31)	46.76 ± 2.22 (31)	17.83 ± 0.50 (31)	0.7 (29)
Ovenbird, *Seiurus aurocapillus*	17.44 ± 1.25 (44)	70.28 ± 2.69 (43)	50.88 ± 2.50 (42)	21.54 ± 0.93 (43)	0.7 (44)
Northern Waterthrush, *S. noveboracensis*	15.53 ± 1.41 (85)	71.22 ± 2.15 (84)	49.28 ± 2.55 (84)	21.08 ± 0.53 (84)	1.0 (86)
Kentucky Warbler, *Oporornis formosus*	12.77 ± 1.11 (60)	63.59 ± 2.55 (59)	45.88 ± 2.62 (59)	21.56 ± 0.73 (59)	1.0 (56)
Common Yellowthroat[b], *Geothlypis trichas*	9.31 ± 0.69 (47)	51.99 ± 2.42 (48)	48.50 ± 2.62 (31)	19.61 ± 0.62 (29)	0.9 (47)
Hooded Warbler, *Wilsonia citrina*	9.41 ± 0.62 (50)	61.55 ± 2.22 (51)	54.64 ± 1.80 (50)	19.12 ± 0.62 (49)	0.4 (49)
Indigo Bunting[b], *Passerina cyanea*	13.50 ± 1.06 (88)	62.40 ± 2.50 (87)	49.33 ± 2.33 (65)	16.85 ± 0.54 (83)	0.9 (84)

[a] Tarsometatarsus.
[b] Entire sample from after 8 October 2001 (the date when Hurricane Iris struck).

TABLE 2. Body mass of woodland migrants mist-netted in Big Falls, Belize, 11 August–15 November 2001.

	Lean mass[a]	Mean mass	Fat-free mass[b]	Lean mass *t*[c]	Fat-free mass *t*[c]
Red-eyed Vireo[d]		16.88	14.59		10.14***
Veery[d]		32.15	26.66		8.92***
Swainson's Thrush	26.5	29.36	24.18	3.34*	23.50***
Wood Thrush	42.0	42.93	42.21	1.12	1.23
Gray Catbird	32.4	34.35	31.80	4.17*	8.17***
Magnolia Warbler	7.0	7.17	6.92	1.87	2.63**
American Redstart	6.75	6.93	6.49	1.11	5.03***
Worm-eating Warbler	12.0	12.27	10.79	1.12	7.17***
Ovenbird	16.7	17.44	15.52	1.94	7.54***
Northern Waterthrush	15.3	15.53	13.68	0.698	9.02***
Kentucky Warbler	12.0	12.77	11.36	2.87*	9.25***
Common Yellowthroat	9.15	9.31	8.36	0.836	5.38***
Hooded Warbler	9.5	9.41	8.2	−0.692	9.37***
Indigo Bunting	13.1	13.50	12.34	1.23	8.76***

[a] Mean mass of individuals with fat score of zero.
[b] Dunning (1993).
[c] $*P < 0.05$; $**P < 0.005$; $***P < 0.0005$.
[d] No Veeries or Red-eyed Vireos had a fat score of zero.

of fat scores with respect to time (Table 3), and all of these species also had significant slopes of mass with respect to time. Kentucky Warblers had significant slopes of mass and fat score with respect to time, and it appeared this species was fattening at the site even though the wing chord condition index regression with respect to time was not significant (Table 3). Tail length condition index in this species had a slope significantly different from zero (Table 3), which was used to obtain an estimate of net daily mass gain. Veeries did not show any other evidence of mass gain besides a significant positive slope in mass with respect to time, and they were excluded from further analyses.

Regressions of wing chord with respect to time for Swainson's Thrushes and Red-eyed

TABLE 3. Relationships between morphological characters and time of capture of individual woodland migrants in Big Falls, Belize mist-netted between 11 August and 15 November 2001. Values are *F*-statistics from linear regressions of the character against time and test the null hypothesis that slope of the linear model was not significantly different from zero. Asterisks indicate $P < 0.05$ for the *F*-test.

	Mensural characters				Condition indices[a]	
Species	Wing chord	Tail length	Mass	Fat	Wing chord	Tail length
Empidonax	0.2	3.1	8.8*	7.7*	9.8*	4.8*
Red-eyed Vireo	5.3*	2.3	8.3*	0.5	4.1*	3.0
Veery	1.9	1.2	4.8*	3.0	3.5	2.8
Swainson's Thrush	8.5*	4.0*	7.9*	13.1*	4.2*	3.2
Wood Thrush	0.2	0.2	0.1	2.8	0.2	
Gray Catbird	2.2	0.2	24.2*	0.6	18.8*	5.0*
Magnolia Warbler	0.4	0.4	6.5*	3.4	7.0*	8.7*
American Redstart	2.2[b]		6.7*	6.6*	6.6*	
Worm-eating Warbler	1.1	1.1	8.6*	1.2	6.5*	4.0
Ovenbird	0.0	0.0	2.1	2.0	2.9	1.6
Northern Waterthrush	0.1	1.8	8.2*	2.8	8.8*	3.1
Kentucky Warbler	3.9	0.5	7.4*	4.4*	3.6	5.2*
Common Yellowthroat	0.2	0.0	0.8	0.4	0.5	1.8
Hooded Warbler	0.0	0.2	1.8	0.2	2.3	1.4
Indigo Bunting	0.0	0.9	4.3*	0.1	5.0*	0.9

[a] Mass divided by morphological character.
[b] Variable not normally distributed.

TABLE 4. Linear models for diurnal change in condition index for woodland migrants[a] at Big Falls, Toledo District, Belize, 11 August–15 November 2001.

Species	*n*	*b*	*m*	SE *m*	*F*	*P*	r^2	Condition gain/day[b]
Empidonax	88	0.14936	0.00260	0.00083	9.8	0.0025	0.11	0.03228
Red-eyed Vireo	39	0.19128	0.00276	0.00136	4.1	0.0504	0.10	0.03427
Veery	66	0.31382	0.00287	0.00154	3.4	0.0675	0.05	[c]
Swainson's Thrush	306	0.29956	0.00133	0.00065	4.2	0.0418	0.01	0.01651
Wood Thrush	45	0.43273	−0.0012	0.00251	0.2	0.6334	0.01	[c]
Gray Catbird	269	0.36757	0.00406	0.00094	18.8	<0.0001	0.07	0.05041
Magnolia Warbler	77	0.11762	0.00106	0.00040	7.0	0.0100	0.09	0.01316
American Redstart	31	0.11017	0.00086	0.00034	6.6	0.0157	0.18	0.01071
Worm-eating Warbler	31	0.17130	0.00160	0.00063	6.5	0.0165	0.19	0.01987
Ovenbird	43	0.23247	0.00146	0.00086	2.9	0.0955	0.07	[c]
Northern Waterthrush	84	0.19323	0.00250	0.00085	8.8	0.0041	0.10	0.03104
Kentucky Warbler[d]	59	0.25142	0.00243	0.00106	5.2	0.0259	0.09	0.03017
Common Yellowthroat	48	0.17598	0.00360	0.00052	0.5	0.4916	0.01	[c]
Hooded Warbler	51	0.14421	0.00085	0.00056	2.3	0.1372	0.05	[c]
Indigo Bunting	87	0.20401	0.00138	0.00062	5.0	0.0274	0.06	0.01714

[a] Equations are $Y = b + mX$, where Y is condition (g/mm), m is slope (condition change/hr), b is the Y intercept, and X is time (hr). F-statistic and corresponding P-value indicate whether the slope differed from zero; r^2 is the coefficient of determination and is a measure of the strength of the relationship between time (X) and condition (Y).

[b] Units are g/mm for the average day length of 12.42 hrs.

[c] Slope not significantly different from zero and gains were not estimable.

[d] Tail condition index used to estimate mass gain.

Vireos revealed a significant positive slope (Table 3), suggesting that larger individuals of these two species were more likely to be captured later in the day. We divided the sample of Swainson's Thrushes in half by wing chord to examine the possibility that wing chord might impart, rather than remove, a size bias when calculating individual condition index values. We tested whether the longer-winged half of our sample had greater condition indices than the shorter-winged half using a one-tailed t-test. There was no difference in condition indices between the two groups (t = 0.62, df = 303, P = 0.27), suggesting the significant relationship of wing chord with time of day in these species was not causing the significant relationship between our wing chord-based condition index and time of day.

Linear models (Table 4) for the 10 taxa that had significant slopes of condition index with respect to time (Table 3) were used to estimate average gross and net daily mass gains (Table 5). Net estimates of mass gain were variable among those species showing gains. For example, average gains for Swainson's Thrush were less than 4% of lean body mass, but in four taxa (*Empidonax*, Gray Catbird [*Dumetella carolinensis*], Red-eyed Vireo, and Northern Waterthrush [*Seiurus noveboracensis*]) our estimates showed net diel mass gains of more than 10% of mean body mass (Table 5).

Flight Capacity Estimates.—Estimates of flight times possible with taxon-average gains varied from <3 to >10 hrs. Average individuals of four taxa (*Empidonax*, Gray Catbird, Red-eyed Vireo, and Northern Waterthrush) were estimated to be capable of flying for between 8 and 11 hrs if all mass gained was fat (i.e., an entire night after just 1 day of fattening; Table 5).

DISCUSSION

Our data suggest that 10 of the 15 taxa studied used this site to acquire resources and gain mass, and that no taxa had significantly negative daily mass gain estimates. The extent of mass gain varied among taxa at the site. All taxa with significant mass gains gained sufficient mass to more than offset estimated nocturnal losses.

The substantial net gain estimates in some taxa (*Empidonax*, Red-eyed Vireo, Gray Catbird, and Northern Waterthrush) suggest that habitat at this site was sufficiently favorable to allow for nearly a full night of migration after only 1 day of feeding; 90% of the taxa had a net gain of at least 5% of lean mass per

TABLE 5. Estimates of daily net increases in mass using wing chord condition index (Kentucky Warbler uses tail condition index) for woodland migrants captured in Big Falls, Toledo District, Belize, 11 August–15 November 2001. Units are g, except where noted.

Species	Gross gain per day[a]	Existence metabolism[b]	Existence metabolism as percentage of lean mass	Net gain per day[c]	Increase as percentage of lean mass	Flight cost (g/hr)[d]	Hours of flight[e]
Empidonax	2.13	0.53		1.60	11.43	0.15	10.82
Red-eyed Vireo	2.57	0.44	2.82	2.13	13.64	0.21	10.10
Swainson's Thrush	1.54	0.61	2.30	0.93	3.51	0.36	2.57
Gray Catbird	4.31	0.69	2.13	3.62	11.18	0.42	8.61
Magnolia Warbler	0.74	0.27	3.86	0.47	6.76	0.09	5.17
American Redstart	0.62	0.26	3.85	0.36	5.31	0.09	4.05
Worm-eating Warbler	1.29	0.37	3.08	0.92	7.65	0.15	5.95
Northern Waterthrush	2.21	0.43	2.81	1.78	11.64	0.19	9.17
Kentucky Warbler	1.38	0.37	3.08	1.01	8.42	0.16	6.29
Indigo Bunting	1.07	0.39	2.98	0.68	5.18	0.17	4.01

[a] Mass gain during 1 day for average individual using average size for wing chord (Kentucky Warbler uses tail length).
[b] Mass loss due to existence metabolism (Kendeigh 1970).
[c] Net 24-hr mass gain after subtraction of nightly mass loss of existence metabolism from gross gain/day.
[d] Cost of flight in g of fat/hr calculated following Tucker (1974:306) using average mass of captured individuals.
[e] Hours of flight possible calculated from Tucker (1974) using an energy value of 30.2 kJ per g (Pennycuick 2003).

day (Table 5). Our estimates are conservative for individuals that stopped for only 1 day and did not spend a night at our site because, as nocturnal migrants, they would lose little to nocturnal resting metabolism, and the amount available for migration would be closer to the gross mass gain estimates.

Only 40% of species with significant mass gain estimates also had significant fat score trends. Fat scores are subjective ordinal estimates of the fat content in birds, not absolute measures, and they estimate only visible subcutaneous deposits on the venter of a bird, even though fat is also deposited in other areas (King and Farner 1965). The association between lipid index (g lipid per g lean dry mass) from fat extractions and fat scores for wintering Dark-eyed Juncos (*Junco hyemalis*) taken by one experienced observer on the same birds was high (r^2 = 0.974; Rogers 1991). Rogers (1991) showed that an experienced observer could detect small changes in fat stores by scoring visible fat, but he cautioned that inter-observer differences in fat scores could affect analyses of fat score data. Fat scores were taken by two observers during our study, and one had not previously used the technique. It is likely the lack of significance in fat score regressions when so many species showed significant mass and condition index gains was, at least in part, due to inter-observer variation and the confounding factor of observer inexperience. Thus, we emphasize these are estimates, but assume that gains in condition index reflect gains in mass.

If the significance of the relationship of wing chord with respect to time could impart a bias to wing chord condition index values, as Winker (1995a) suggested might occur, one would expect a significant difference between the mean condition indices of the larger (longer-winged) individuals and the smaller (shorter-winged) individuals. Our analysis of Swainson's Thrushes, showing the longer-winged half of our sample did not have different condition indices than the shorter-winged half, demonstrated concern about a possible failure of this methodology is unwarranted.

The year-to-year variability at this site cannot be addressed with these data, especially since the site was severely altered by Hurricane Iris. Species with significant daily gains in 1 year in Minnesota during a 3-year study often showed significant gains in more than 1 year (Winker 1995a). However, Dunn (2000) has shown significant differences in mass gains among years at a single site in a single species. Habitat damage caused by Hurricane Iris may have changed the suitability of the site for some migrants, although it is notable that four of the six species in our sample still had significant mass gains at this site after Hurricane Iris.

Species such as Veery and Swainson's Thrush, whose winter ranges are entirely or largely in South America, might have been expected to be fattening as much as Red-eyed Vireos, which also winter entirely in South America. A migration strategy that would account for low levels of fattening is that higher resource certainty in the tropics compared to temperate habitats might not require depositing large amounts of fat; individuals may even be less likely to fatten if they are already close to their winter destinations (Winker 1995a). However, this hypothesis does not seem to apply to Veeries and Swainson's Thrushes, which were generally carrying large amounts of fat at our site (Table 1). This may explain why Veeries apparently were not fattening at the site (Table 3) and Swainson's Thrushes had the lowest estimate of all fattening species (Table 5), even though they were among the species with the farthest minimum distance yet to travel. The significant differences in several species between lean or fat-free mass and mean mass at our site (and the generally heavy fat loads for several species; Table 1) demonstrate that stopover sites farther north are important areas for fattening for some species. Where the species that arrive fat obtain this fat, and why some species arrive fatter than others, remain important ecological and evolutionary questions.

The high level of fattening by some species and the high level of fat already carried by others is similar to the amount of fattening observed in migrants preparing to make western trans-Atlantic flights from New England (e.g., Nisbet et al. 1963) and trans-gulf flights from the central coast of the Gulf of Mexico (Woodrey and Moore 1997). This is in contrast to the generally low levels of fattening observed in other, mid-continental studies (Winker et al. 1992, Dunn 2002), and is different from the low levels of fattening observed by Winker (1995a) on the Isthmus of Tehuantepec. The high levels of fat observed at our site may be in preparation for a long-distance migratory flight, rather than shorter flights south through Central America. The emaciated migrants observed by Rogers and Odum (1966) in Panama would seem to suggest they arrived from a great distance, also supporting the possibility of longer flights over Central America, rather than shorter flights through it. Mass gain data from farther south in Central America would be useful in elucidating this situation.

Our study suggests that lowland forests in the southeastern Yucatan Peninsula are important to many species of transient migrants as an area to build fuel stores. Some species showed average trends of depositing sufficient fat in 1 day for an entire night of migration. However, some species arrived at this site carrying substantial fat loads apparently from farther north. This study combined with other studies of fattening and stopover ecology of Nearctic-Neotropic migrants is helpful for developing hypotheses about geographic variation and interspecific differences in fuel deposition strategies in the Nearctic-Neotropic migration system. Much work remains to be done in many of these same areas during spring migration, and there are few or no published data collected during any season from South America, Central America between Belize and Panama, or the southeastern United States. It does appear that more than one strategy for fattening in northern Central America has evolved among passerine migrants.

ACKNOWLEDGMENTS

This study was funded by the University of Alaska Museum, the U.S. Department of Agriculture (SCA 58-6612-8-022), an anonymous donor, and the University of Alaska Fairbanks Graduate School. Able field assistance was provided by Santos Hun. Critical support in Belize was provided by Donald Owen-Lewis, the Francisca Bardalez family, the Cantel Hun family, Peter Dunham, and K. M. Prufer. Personnel in the Conservation Division of the Forest Department in Belize provided permits to conduct the research and working with them was a pleasure. A. N. Powell, D. L. Thomas, E. C. Murphy, E. H. Dunn, and two anonymous reviewers provided helpful editorial suggestions and statistical advice. D. M. Johnson served as our botanical consultant.

LITERATURE CITED

American Ornithologists' Union (AOU). 1998. Check-list of North American birds. Seventh Edition. American Ornithologists' Union, Washington, D.C., USA.

Bauchinger, U. and H. Biebach. 2000. Differential catabolism of muscle protein in Garden Warblers (*Sylvia borin*): flight and leg muscle act as a protein source during long distance migration. Journal of Comparative Physiology B 171:293–301.

Child, G. I. 1969. A study of nonfat weights in mi-

grating Swainson's Thrushes (*Hylocichla ustulata*). Auk 86:327–388.

Connell, C. E., E. P. Odum, and H. Kale. 1960. Fat-free weights of birds. Auk 77:1–9.

Dunn, E. H. 2000. Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. Auk 117:12–21.

Dunn, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson Bulletin 114:368–379.

Dunning Jr., J. B. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, Florida, USA.

Freeman, S. and W. M. Jackson. 1990. Univariate metrics are not adequate to measure avian body size. Auk 107:69–74.

Galindo, P. and E. Mendez. 1965. Banding of thrushes and catbirds at Almirante, Panama. Second year of observations. Bird-Banding 36:233–239.

Galindo, P., E. Mendez, and A. J. Adames. 1963. Banding of migrant thrushes in Almirante, Panama. Bird-Banding 34:203–209.

Helms, C. W. and W. H. Drury. 1960. Winter and migratory weight and fat field studies of some North American buntings. Bird-Banding 31:1–40.

Karasov, W. H. and B. Pinshow. 1998. Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71:435–448.

Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of bird. Condor 72:60–65.

King, J. R. and D. A. Farner. 1965. Studies of fat deposition in migratory birds. Annals of the New York Academy of Sciences 131:422–440.

Monroe Jr., B. L. 1968 A distributional survey of the birds of Honduras. Ornithological Monographs 7.

Nisbet, I. C. T., W. H. Drury Jr., and J. Baird. 1963. Weight-loss during migration. Part I. Deposition and consumption of fat by the Black-poll Warbler *Dendroica striata*. Bird-Banding 34:107–138.

Pennycuick, C. J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press, Oxford, United Kingdom.

Pennycuick, C. J. 2003. The concept of energy height in animal locomotion: separating mechanics from physiology. Journal of Theoretical Biology 224: 189–203.

Rising, J. D. and K. M. Somers. 1989. The measurement of overall body size in birds. Auk 106:666–674.

Rogers, C. M. 1991. An evaluation of the method of estimating body fat by quantifying visible subcutaneous fat. Journal of Field Ornithology 62:349–356.

Rogers, D. T. and E. P. Odum. 1964. Effect of age, sex, and level of fat deposits on major body components in some wood warblers. Auk 81:505–513.

Rogers, D. T. and E. P. Odum. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. Wilson Bulletin 78:415–433.

Stiles, F. G. and D. L. Altshuler. 2004. Conflicting terminology for wing measurements in ornithology and aerodynamics. Auk 121:973–976.

Tucker, V. A. 1974. Energetics of natural avian flight. Publications of the Nuttall Ornithological Club 15:298–333.

Winker, K. 1995a. Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic-Neotropic migrants. Auk 112:690–700.

Winker, K. 1995b. Neotropical stopover sites and Middle American migrations: the view from southern Mexico. Pages 150–163 *in* Conservation of neotropical migratory birds in Mexico (M. Wilson and S. Sader, Editors). Miscellaneous Publication. Maine Agricultural and Forestry Experiment Station, Orono, USA.

Winker, K., D. W. Warner, and A. R. Weisbrod. 1992. Daily mass gains among woodland migrants at an inland stopover site. Auk 109:853–862.

Woodrey, M. S. and F. R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. Auk 114:695–707.

The Wilson Journal of Ornithology 120(2):286–295, 2008

NUMBERS OF MIGRATORY BIRDS STOPPING OVER IN NEW ORLEANS, LOUISIANA, USA IN RELATION TO WEATHER

PETER H. YAUKEY[1,2] AND SHAWN C. POWELL[1]

ABSTRACT.—Migratory birds were surveyed at stopover sites in New Orleans, Louisiana, during seven spring and fall seasons in relation to weather conditions. Weather was classified into four synoptic scenarios distinguished primarily by positions of fronts, wind directions, and pressure characteristics. Overall numbers of migrants in spring were more numerous during the synoptic scenarios in which a cold front was about to arrive (Frontal Gulf Return) or had already passed (Post Frontal), than when airflow was off the Gulf or from the east (Coastal Return, which often preceded frontal passage). Counts of White-eyed (*Vireo griseus*) and Red-eyed vireos (*V. olivaceus*), Indigo Buntings (*Passerina cyanea*), and thrushes (*Hylocichla* and *Catharus* combined) showed differences among weather scenarios, mostly with high counts under Post Frontal conditions and/or low counts under Coastal Return. Post Frontal values were higher in fall than Coastal Return for overall migrants, Common Yellowthroats (*Geothlypis trichas*), and Indigo Buntings. However, four individual species failed to show any variation with weather. Counts after cold front passages in both spring and fall were higher than those preceding the fronts for all migrants combined. *Received 29 July 2004. Accepted 27 September 2007.*

Studies of the ecology and behavior of migratory birds during passage are important, given the significance of the migratory journey in their annual cycles. A key component of the migratory strategies of migrants is use of stopover sites for resting, re-hydrating, and refueling during their journeys, as well as finding protection from predators. The number of birds using a given site can vary dramatically from day to day; weather has long been thought to have a key role in daily variations in numbers of birds migrating and occurring at stopover sites (reviewed by Lack 1960; Richardson 1978, 1990).

The number of birds occurring at a stopover site on a given day is a function of several variables including the volume of migration on the preceding night or nights, and decisions made by birds using the site on previous dates whether to depart or remain another day. Both are influenced by weather; good migratory weather can bring migrants in and stimulate others to depart. Substantial research has been devoted to the impact of weather on migration and researchers have arrived at a consensus regarding basic weather conditions that favor migration (e.g., Lack 1960; Richardson 1978, 1990; Alerstam 1990; Berthold 1993). For instance, fall migration is heaviest under conditions of rising or high pressure and gentle or following (northerly) winds, as often occur following cold front passage. These studies have associated spring migration with tail winds as well, but these are southerly and often associated with decreasing pressure. Precipitation is generally unfavorable for migration. This fall scenario applies to New Orleans, Louisiana, but spring migration is somewhat different due to the location of the city, 100 km inland from the Gulf of Mexico. First, the southerly latitude of New Orleans causes new arrivals to approach across tropical and low subtropical latitudes over the Gulf of Mexico where weather patterns differ from those of the mid latitudes where most other studies have been conducted. Second, most trans-Gulf migrants in spring do not arrive in the vicinity of New Orleans until well into the daylight hours; they have been shown to mostly fly well inland past New Orleans before alighting (Lowery 1945, Gauthreaux 1971). The lack of birds stopping over in near-coastal areas of Louisiana has led to these areas being labeled the "coastal hiatus" (Lowery 1945). It is reasonable to expect that migration over the Gulf is strongest when there are tailwinds (southerly) and no rain. Gulf Coast observers (e.g., Duncan 1994) have generally perceived that numbers of birds alighting in near-coastal areas such as New Orleans are greatest when a cold front penetrates the Gulf, presenting inclement weather for northbound trans-Gulf migrants causing them to stop near the coast rather than travel farther inland as usual.

[1] Department of Geography, University of New Orleans, New Orleans, LA 70148, USA.

[2] Corresponding author; e-mail: pyaukey@uno.edu

Our overall objective was to examine the effect of weather on number of migratory birds stopping over in New Orleans, Louisiana. We compared numbers of migrants among different synoptic conditions before and after passage of cold fronts based upon an existing weather classification system (Muller 1977). Peak numbers in spring were predicted under conditions that cause northbound migrants to "stall" in New Orleans (cold front passage, bringing inclement weather into the paths of northbound trans-Gulf migrants). We did not predict which scenarios would have the highest counts in fall, because cold front passages could either elevate stopover bird counts by stimulating arrival of birds, or lower them by stimulating departure.

METHODS

Bird Surveys.—Migrant birds were counted on 15 survey transects in two urban residential neighborhoods and two city parks within New Orleans, Louisiana. One neighborhood (6 transects) was typical of New Orleans and had relatively sparse vegetation density, while the other (3 transects) was among the most-vegetated residential areas of the city. Residential transects were along quiet roads and alleys. One park (2 transects, 2.5 ha) had an extensive tree canopy, but no understory vegetation or ground cover; the other park site (4 transects) was a 13-ha woodlot with a basically intact understory, especially of camphor trees (*Cinnamomum camphora*), exotic elms (*Ulmus* spp.), and giant ragweed (*Ambrosia trifida*). The dominant canopy trees on the four sites were live oak (*Quercus virginiana*), water oak (*Q. nigra*), Nuttall oak (*Q. nuttallii*), hackberry (*Celtis laevigata*), Chinese tallow (*Sapium sebiferum*), pecan (*Carya illinoënsis*), magnolia (*Magnolia* spp.), sweetgum (*Liquidambar styraciflua*), loblolly pine (*Pinus taeda*), and slash pine (*P. ellioti*). The most distant sites were 6 km apart. The urban context of this study may have caused the sampling area to be avoided by some migrants if they perceived the area to be low quality stopover habitat.

Transects were straight lines 200 m in length; 3 min were spent walking each and all migratory birds seen or heard within 25 m were recorded. The primary author conducted all bird surveying. This relatively rapid pace of coverage was designed to maximize the number of migrants encountered, which pilot surveys indicated might be accomplished by using a relatively fast pace to maximize the area surveyed. The fast pace allowed all 15 transects to be covered on each survey date, eliminating coverage differences among days and maximizing comparison of migrant counts made on different dates.

Transects were surveyed before 4.5 hrs after sunrise, except on 10 days when surveying occurred later (ending within 7 hrs after sunrise) due to rain. Gauthreaux (1971) detected some spring trans-Gulf migrants arriving over New Orleans in the early morning, but normally peaking after 1200 hrs CST. The large majority of birds counted in spring were probably arrivals from previous days. The sequence of visitation of the four sites was rotated each visit. Serial autocorrelation was minimized by allowing 2–3 days to elapse between consecutive surveys, a time span similar to previously reported mean multiple-day stopover lengths of captured migrants in spring in non-urban habitats on the Gulf Coast (Moore and Kerlinger 1987, Loria and Moore 1990). The number of instances of the same species being recorded on the same transect on consecutive visits was calculated at the end of the season to conservatively assess the maximum possible rate of repeat observations of the same individuals.

Surveying was conducted from ~15 March to 15 May each spring and 20 August to 31 October each fall from 1994 to 2000. Birds were not surveyed during high winds or heavy rains. All species that breed on or near the study sites were excluded to restrict the spring analysis to passage migrants—including Mississippi Kite (*Ictinia mississippiensis*), Yellow-billed Cuckoo (*Coccyzus americanus*), Great Crested Flycatcher (*Myiarchus crinitus*), Eastern Kingbird (*Tyrannus tyrannus*), Purple Martin (*Progne subis*), and Bronzed Cowbird (*Molothrus aeneus*). Most species that winter in the southeastern United States were also excluded from both spring and fall analyses because they wintered in or near the study area, although the absence of wintering Blue-headed Vireo (*Vireo solitarius*), Winter Wren (*Troglodytes troglodytes*), Gray Catbird (*Dumetella carolinensis*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Common Yel-

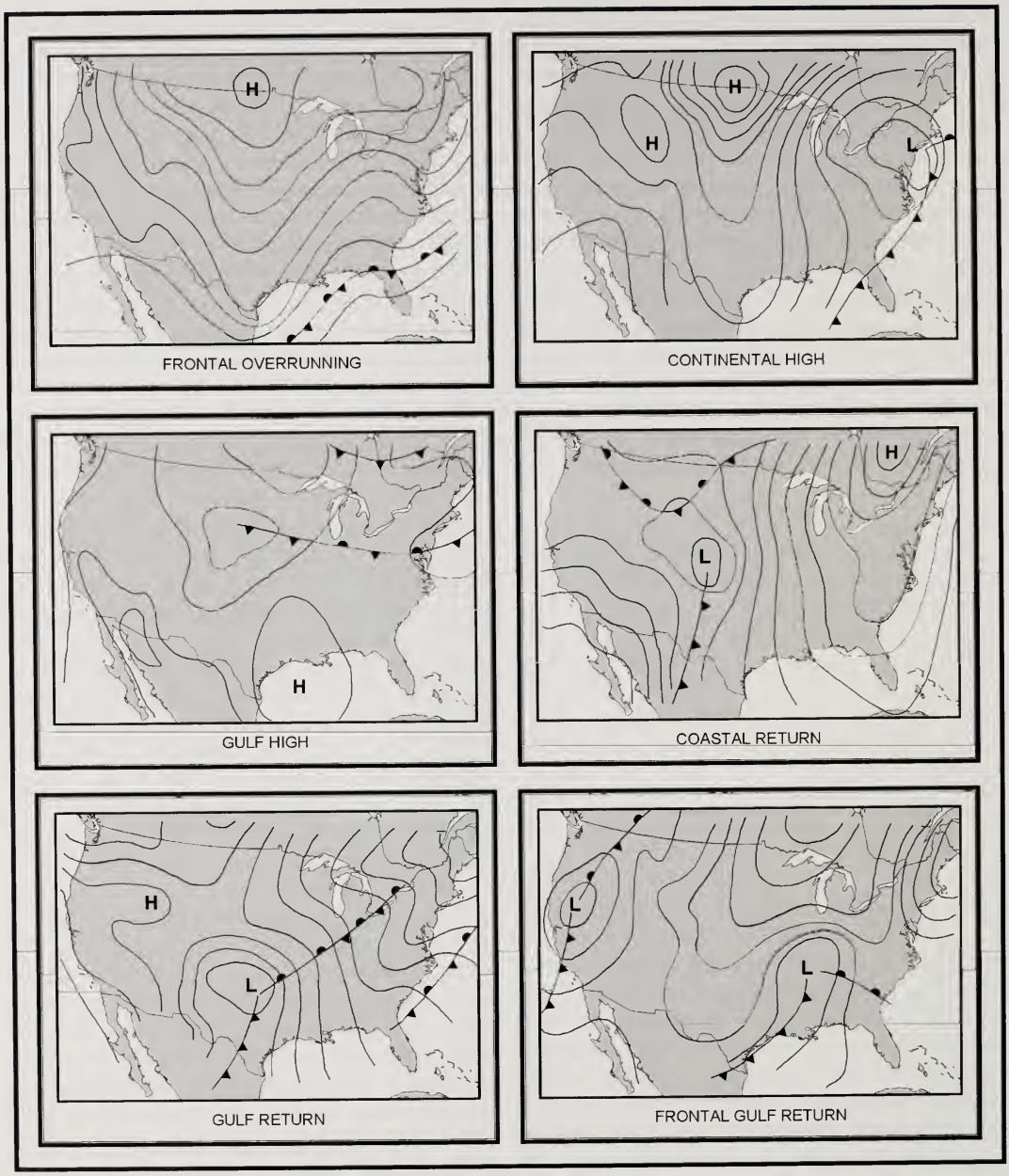


FIG. 1. Synoptic weather categories (after Muller 1977). Map by Eric Bock.

lowthroat (*Geothylpis trichas*), Wilson's Warbler (*Wilsonia pusilla*), and Eastern Towhee (*Pipilo erythrophthalmus*) allowed their inclusion.

Weather Condition Categories.—Muller (1977) devised an eight-category classification system for describing weather conditions in Louisiana and the *Louisiana Monthly Climate Review* has published daily classifications of the 0600 and 1500 hrs CST conditions for several cities in Louisiana on an ongoing basis. Muller's categories are based upon positions of fronts, wind directions, and other criteria (Fig. 1). Six categories are commonly related to the sequence of weather changes as a cold front approaches: an easterly airflow

occurring while an approaching cold front is still distant is typical of the "Coastal Return" scenario, which transitions into the "Gulf Return" scenario with more southerly flow as the front draws closer. "Frontal Gulf Return" and "Frontal Overrunning" scenarios occur immediately before and after the frontal passage, respectively, and are followed by "Continental High" conditions in the fair weather and high pressure after the front. When the ridge is (infrequently) centered west of the Rockies, the post-frontal high pressure is termed a "Pacific High." These synoptic types at times occur outside this frontal sequence, but the Continental High and Frontal Overrunning are closely associated with post-frontal conditions; in both spring and fall, >90% of the occurrence of each in this study was immediately after a cold frontal passage (i.e., before the appearance of other weather types, but infrequently occurring with Pacific High). Gulf Return and Coastal Return are the scenarios most different from those following a cold front passage (i.e., the least likely to have northerly winds). They are also the conditions most likely to precede a cold front passage. Two additional categories are used that do not fit into a scheme of frontal passage: "Gulf High" when weather is dominated by a high pressure cell in the Gulf, and "Gulf Tropical Disturbance" when influenced by a tropical low or storm in the Gulf. These eight categories were simplified to four for our analysis: Frontal Overrunning and Continental High were combined into a category labeled "Post Frontal," Gulf and Coastal Return were combined and labeled "Coastal Return," and Frontal Gulf Return and Gulf High were used without alteration. Pacific Highs and Gulf Tropical Disturbances were infrequent and omitted from statistical analyses.

Statistical Analyses.—Numbers of migrant birds were compared among four synoptic categories of climate using Krukal-Wallis tests with accompanying multiple comparison tests (Zar 1984). The number of migrants passing through New Orleans changes as spring or fall progresses, which could complicate simple comparison of bird numbers among synoptic types (whose numbers and magnitude of day to day variations also might vary through the migration seasons). Thus, numbers of birds recorded on each daily survey were "corrected" for these factors by subtracting from each the "normal" seasonal abundance level (estimated by calculating 5-day means for each date from the 7 years of data in the study), and dividing this residual by the standard deviation of those same counts. Autumnal migrants in New Orleans might be influenced by weather conditions to the north which they fly through during their nocturnal migratory flight. Thus, these "corrected" migrant numbers were compared among different synoptic categories of weather occurring at Monroe, Louisiana, 350 km NNW of New Orleans, on the afternoon before the survey date. This was the most northerly station at which synoptically classified weather data were available.

The most abundant species of migrants for spring and fall seasons were analyzed independently in addition to analyzing total numbers of migrants. Analyses of individual species were confined to surveys within their normal times of passage, excluding dates earlier and later than their extremes of occurrence over the 7 years. Weather analyses for Yellow Warblers (*Dendroica petechia*) and American Redstarts (*Setophaga ruticilla*) were confined to on or before 10 September and on or after 1 October, respectively, to avoid potential confusion of their vocalizations during their period of overlap (assessed by visual observations of the species).

Bird numbers were also compared before and after passage of cold fronts depicted in the publication *Daily Weather Maps* in addition to Muller's (1977) synoptic categories (U.S. Department of Commerce, 1994–2000). Any frontal boundary that passed New Orleans from north to south was included in the analysis even if it was designated a stationary front in *Daily Weather Maps.* We compared the raw (uncorrected) number of migrants for the last survey prior to each front with the first survey following it using a paired Student's *t*-test. Correction of numbers for seasonal variations in abundance was not considered necessary for this analysis since the two counts compared were on similar dates in each case. Neither front was included in the analysis if more than one front (including warm fronts) passed New Orleans between consecutive migrant surveys.

TABLE 1. Synoptic weather classification system for New Orleans, Louisiana, USA (after Muller 1977) with number of survey dates (*n*) on which each occurred over the 7 years of study.

Type	Spring (*n*)	Fall (*n*)	Description
Coastal Return[a]	13	46	Winds veer from northeast to southeast as ridge drifts eastward (spring) or have easterly component when Bermuda High extends into southeastern U.S. (fall).
Gulf Return[a]	62	38	Winds veer to southeast and south as air is drawn off Gulf by ridge drifting farther east or in front of low advancing from Texas panhandle; front distant.
Frontal Gulf Return	23	13	Front nearby; return flow in warm sector of system.
Frontal Overunning[b]	24	17	Polar front stationary along Gulf Coast/northern Gulf.
Continental High[b]	27	52	High pressure center usually east of Rockies; northerly flow; fair and cool to cold weather associated with core of high.
Pacific High	4	2	High center usually over eastern Pacific or west of Rockies; mild and dry air after cold front.
Gulf High	8	14	Southwestern flow associated with western extension of high over Gulf; in summer often extension of Bermuda High.
Gulf Tropical Disturbance	1	18	Influenced by tropical disturbances ranging from easterly waves to hurricanes.

[a] Combined for statistical analyses into a single category, "Coastal Return".
[b] Combined for statistical analyses into a single category, "Post Frontal".

RESULTS

Synoptic Weather During Spring Passage.—During the seven springs of the study, 998 migrants were recorded on the 173 survey dates. Only 4.9% of the birds counted were on the same transect as an individual of the same species on the previous census date. This total includes all conspecifics not just duplicate observations of a single individual. It is not known how the mean stopover length of birds compared to the interval between visits but, because the number of potential repeat observations of the same individual birds was small, it was assumed that serial autocorrelation was unimportant.

The most common synoptic scenarios at New Orleans in spring were the Coastal Return (air being drawn from the east or off the Gulf, often as a cold front approached) and Post Frontal (Table 1). The frequency of occurrence of each scenario varied markedly from year to year; Coastal Return conditions prevailed on 26 to 65% of days in any year, Frontal Gulf Return conditions (cold front near but not yet passed) varied from 4 to 24%, Post Frontal ranged from 17 to 48%, and Gulf High from 0 to 14%. The typical pattern was for migrants to be scarce on most days, punctuated by occasional days with increased counts, and on some occasions by spectacular numbers. Two or fewer migrants were recorded on 51% of the days with none on 23%; counts of ≥30 migrants were recorded on only 4% of survey dates. The latter group typically represented "fallout" days when hundreds of individuals were present on and near the transects, even though the highest daily count used for statistical analyses only reached 49 because of the strict survey protocol, and because many migrants were excluded because their species also wintered on the site (e.g., Yellow-rumped Warbler [*Dendroica coronata*]).

The number of spring migrants (corrected using mean and standard deviation) varied depending on the synoptic scenario present in New Orleans on the morning of the survey (Kruskal-Wallis, $\chi^2 = 23.19$, $n = 155$, $P < 0.001$). However, the synoptic conditions present the previous afternoon showed an even stronger pattern with respect to corrected count numbers ($\chi^2 = 30.06$, $n = 155$, $P < 0.001$; Table 2). Trans-Gulf migrants typically arrive in New Orleans well into the daylight period and early morning surveys largely counted birds that arrived the previous day. Thus, the following analyses were based upon the synoptic conditions present the afternoon before each survey.

TABLE 2. Tests for differences in the number of spring migrants recorded when different synoptic weather scenarios existed at 1500 hrs the previous day.

	Dates	n[a]	Kruskal-Wallis χ^2	P	Significantly different scenarios[b]
White-eyed Vireo	17 Mar–12 May	153	18.82	<0.001	Post>Coastal, Post>FGR
Red-eyed Vireo	28 Mar–14 May	127	14.00	0.003	Post>Coastal
Thrush spp.	1 Apr–12 May	112	15.60	0.001	GH>Coastal, FGR>Coastal
Hooded Warbler	27 Mar–4 May	103	4.06	0.255	None
Indigo Bunting	28 Mar–14 May	127	12.80	0.005	Post>GH, FGR>GH
All migrants	17 Mar–14 May	157	30.06	<0.001	Post>Coastal, FGR>Coastal

[a] Number of survey days within period of occurrence.
[b] Coastal = Coastal Return (air flow from Gulf Coast); FGR = Frontal Gulf Return (cold front approaching); Post = Post Frontal (following passage of a cold front); GH = High pressure cell in Gulf.

Coastal Return bird numbers (corrected) were significantly lower than for both Frontal Gulf Return (Q = 3.84; Qcritical = 2.64) and Post Frontal (Q = 4.84) conditions. These are normally conditions in which a front is arriving at or has passed New Orleans.

The four most numerous species recorded in spring were Indigo Bunting (*Passerina cyanea*), Red-eyed Vireo (*Vireo olivaceous*), White-eyed Vireo (*V. griseus*), and Hooded Warbler (*Wilsonia citrina*). Numbers of each of these species, except Hooded Warbler, varied significantly among the different synoptic scenarios (Table 3). Frontal Gulf Return (Q = 2.69) and Post Frontal (Q = 2.89) conditions recorded higher corrected counts for Indigo Bunting than did Gulf High. Coastal Return conditions were also lower than Frontal Gulf Return and Post Frontal, but not significantly. Coastal Return counts for Red-eyed Vireo were significantly lower than Post Frontal counts (Q = 3.44). White-eyed Vireo counts were higher under Post Frontal conditions than either Coastal Return (Q = 3.80) or Frontal Gulf Return (Q = 3.02). These scenarios recorded similar numbers, suggesting numbers of this species did not increase when a front was arriving. Coastal Return numbers were significantly lower than Frontal Gulf Return (Q = 2.69) and Gulf High (Q = 3.07) numbers for thrushes.

Synoptic Weather During Fall Passage.—A total of 1,197 migrants was recorded on 211 survey dates over the seven fall periods. During fall, only 14.7% of individuals were on the same transect as a bird of the same species on the previous survey. Thus, it was presumed that serial autocorrelation was not a serious problem, because these can represent different individuals.

The most common synoptic scenarios in fall were Coastal Return and Post Frontal (Table 1). The number of Coastal Return days varied annually between 35 and 54%, and Frontal Gulf Return between 4 and 15%. Between 26 and 44% of days had Post Frontal

TABLE 3. Tests for differences in numbers of fall migrants recorded when different synoptic weather scenarios existed at 1500 hrs the previous day.

	Dates	n[a]	Kruskal-Wallis χ^2	P	Significantly different scenarios[b]
Eastern Wood-Pewee	21 Aug–28 Oct	172	3.34	0.342	None
Gray Catbird	23 Sep–29 Oct	100	5.47	0.140	None
Yellow Warbler	21 Aug–10 Sep	48	1.39	0.707	None
American Redstart	1 Oct–27 Oct	74	1.78	0.620	None
Common Yellowthroat	25 Aug–29 Oct	168	15.74	0.001	Post>Coastal
Indigo Bunting	22 Sep–29 Oct	130	10.63	0.014	Post>Coastal
All migrants	21 Aug–29 Oct	176	10.60	0.014	Post>Coastal

[a] Number of survey days within period of occurrence.
[b] Coastal = Coastal Return (air flow from Gulf Coast); FGR = Frontal Gulf Return (cold front approaching); Post = Post Frontal (following passage of a cold front); GH = High pressure cell in Gulf.

conditions each year, and between 0 and 19% were Gulf High days. Numbers of migrants in fall were highly variable from day to day with only 6% of survey dates exceeding 30 systematically-counted migrants (corresponding to large numbers at the site). However, there were many fewer days with ≤2 (10%) or none (1%) detected than in spring. The norm in fall was to have small numbers, but not as small as in spring.

Numbers of fall migrants did not vary when different synoptic conditions were present at 0600 hrs in New Orleans ($\chi^2 = 6.54$, $n = 178$ dates; $P = 0.088$), but did vary when different scenarios had been present at 1500 hrs the previous afternoon (less strongly than in spring, $P = 0.014$, Table 3). More migrants were found under Post Frontal than Coastal Return conditions (Q = 3.19; Qcritical = 2.64). Bird numbers did not vary in association with the 1500 hrs conditions the previous afternoon in Monroe, Louisiana, 350 km NW of New Orleans ($\chi^2 = 7.05$, $n = 188$ dates; $P = 0.07$).

The most numerous species in fall were Eastern Wood-Pewee (*Contopus virens*), Gray Catbird, Yellow Warbler, American Redstart, Common Yellowthroat, and Indigo Bunting. In contrast to spring, only two species had significant variation in numbers among scenarios of synoptic weather (Table 3). Both Common Yellowthroat (Q = 3.72) and Indigo Bunting (Q = 3.06) were more numerous in Post Frontal than Coastal Return situations.

Cold Fronts in Spring and Fall.—The total number of migrant individuals detected in spring was greater in the first survey following each cold front passage than in the survey prior to each front (mean = 62% increase; paired $t = 2.04$, $n = 53$, $P = 0.023$). Approximately 40% of these fronts were weak and showed signs of stalling before or after passing New Orleans. Weak fronts might be expected to have less effect on migrants, but their omission did not support this assumption (mean for strong fronts = 48% increase; paired $t = 1.15$, $n = 31$, $P = 0.13$).

The number of migrant individuals in fall was greater following cold front passage than prior to it (mean = 48% increase; paired $t = 2.16$, $n = 43$, $P = 0.018$). Of these fronts, 50% showed signs of stalling in fall and omission of these weak fronts revealed an even stronger pattern for the strong fronts (mean for strong fronts = 93% increase; paired $t = 3.14$, $n = 22$, $P = 0.003$).

Gulf Tropical Disturbances.—Numbers of birds were greater under tropical disturbance conditions (0600 or 1500 hrs) than any other scenario. However, these differences were not significant, and patterns of individual species were complicated. Mornings following tropical disturbance conditions in New Orleans ranked lower than any other synoptic scenario for Common Yellowthroats ($n = 12$ dates with Gulf Tropical Disturbances) and Yellow Warblers ($n = 8$), but second highest for Eastern Wood-Pewees ($n = 16$ dates). Too few Gulf Tropical Disturbances occurred during the relatively late migratory periods of Gray Catbirds and Indigo Buntings to suggest patterns for those species.

Big Days in Spring and Fall.—The occurrence of migrants in New Orleans in both spring and fall was punctuated by occasional days when exceptional numbers stopped over. Daily transect counts in spring exceeded 30 migrants on seven dates, peaking at 49 on 4 May 1995. Three of these dates were in 1995; none occurred in 1998 or 1999. All 7 days were associated with frontal activity in the Gulf. These counts were only a small sample of the hundreds of birds that appeared to be present on each day.

Peak counts in fall were somewhat higher than in spring and exceeded 40 on seven dates, peaking at 64 on 21 October 1998. All of these dates were associated with frontal passages and/or tropical disturbances.

Interaction of Synoptic Scenario Frequency with Bird Numbers.—The mean number of birds recorded in fall was highest on days with Post Frontal conditions. However, this did not translate into larger season-long migrant counts during falls with more Post Frontal days. The percentage of Post Frontal days each fall (which ranged from 26 to 44% of the survey dates) was *negatively* correlated with the season-long mean daily count of migrants (each day adjusted for means and standard deviations; Spearman's $r = -0.85$, $P = 0.015$). Driving this finding was a strong negative correlation between the percentage of Post Frontal days each fall and the mean count of migrants on these days ($r_s = -0.93$, $P = 0.003$). The low seasonal counts for fall surveys with

many Post Frontal days, despite the high average counts on Post Frontal days overall, might be explainable by variations in the duration of high pressure following cold front passages from year to year. If high counts occur on the first few days after the onset of Post Frontal conditions, followed by reduced numbers as the high pressure continues, fall surveys with long stretches of Post Frontal conditions might record a large number of low counts. This might happen if the number of arrivals declines over time (perhaps having been concentrated immediately behind the front), while favorable winds for departing across the Gulf continue. Numbers of migrants recorded early in strings of Post Frontal weather were higher (counts for days 1–3 averaged 0.27–0.57 standard deviations above their seasonal means) than numbers on days 4–6 of such strings (ranging from −0.13 to −0.69 standard deviations *below* their means). No other synoptic scenario recorded bird counts that varied with their number of days of occurrence, either when considering total seasonal bird counts for all weather types, or just counts on days with their own synoptic conditions, in spring or fall (all $P \geq 0.15$). Gulf High was not included in this portion of the analysis, because it was unrecorded in three spring and two fall periods.

DISCUSSION

We found differences in the number of birds present under different synoptic weather scenarios near the north coast of the Gulf of Mexico despite the increased complexities involved in relating weather to stopover numbers near the edges of ecological barriers (Simons et al. 2004). In spring, most birds were recorded stopping over under two synoptic scenarios: one of which was associated with approaching cold fronts and the other with conditions following frontal passage. The post-frontal scenario also recorded the largest bird counts in fall. In both seasons, numbers were smaller under a weather scenario with winds from the east or off the Gulf.

The results of our study are consistent with perceptions in the literature (Lowery 1945, Dennis 1954, Gauthreaux 1971, Duncan 1994) and more anecdotal accounts that largest numbers of migrant birds stop over along the northern Gulf Coast when there is inclement weather to impede passage over or near the Gulf in spring, and in the tail winds immediately following cold frontal passages in autumn. We provide confirmation of these patterns through systematic quantification of bird numbers over several seasons, which has been generally lacking previously. These patterns are generally consistent with the findings of other studies of the effects of weather on migration (Lack 1960; Richardson 1978, 1990), such as increased movement during tail winds or avoidance of rain. Further studies are needed to compare stopover patterns in an urban setting such as ours, to a broader variety of habitats and geographical contexts.

Previous authors have noted that weather conditions over the Gulf of Mexico are generally favorable for northward migration in spring, but less frequently favorable for southbound migration in fall (Able 1972, Gauthreaux et al. 2005). This may be expected to make stopover bird counts more clearly impacted by weather in fall, when bird movements may be more tightly clustered in the fewer days of favorable migratory conditions. In contrast, migrant counts in our study differed more among weather scenarios in spring than in fall. The greatest impact of weather on stopover numbers near the Gulf Coast may be in grounding migrants with inclement weather (when frontal systems intercept northbound birds in spring), rather than in stimulating migration to begin (as suggested for fall). It is difficult to imagine situations in which fall migrants might encounter inclement weather that might cause grounding, but tropical disturbances may be a good candidate. Gulf Tropical Disturbances in our study showed mixed patterns—associated with relatively high numbers of birds overall and with some of the big days in fall, but also with low numbers of particular species. The winds and rain of a Gulf disturbance may well be capable of producing significant fallouts, but only when other conditions are favorable (tail winds to bring birds into the region, etc.).

Numbers of migrants in spring varied more strongly with weather conditions of the previous afternoon than weather existing at the time of the field survey. This is consistent with the general understanding that spring migrants arrive well into the daylight hours, having still been over the Gulf when daylight ar-

rived (Gauthreaux 1971). Thus, an early morning survey will largely record birds that arrived the previous day and spent the night. The numbers of migrants in fall likewise varied more strongly with weather conditions the previous afternoon, presumably because this reading indicated what weather conditions (e.g., frontal passages) were established in time for the nocturnal flight. The morning of the census might reflect weather that was not yet present when the birds were migrating at night.

One advantage of stopover studies relative to radar studies of migration is the ability to distinguish individual species. Three of the six species examined in fall gave no hint of weather-based differences in counts, despite an overall strong variation of the total migrant count among synoptic features. This highlights the need for more species-specific studies involving stopover observations and the perils of pooling the migratory behavior of all species together, as is necessary in radar studies. One source of interspecific differences in weather-dependence could be the different migration schedules of different species. Yellow Warblers showed no variation among weather patterns; the overwhelming majority of their records were in August when few cold fronts passed New Orleans. It is logical that early migrants would have migratory strategies not heavily dependent upon frontal systems, which are infrequent early in the fall. White-eyed Vireo counts suggested a lack of elevated numbers in spring under Frontal Gulf Return conditions, and Eastern Wood-Pewee numbers appeared to be unusually high during Gulf High conditions in fall, trends atypical of the overall migrant pool and worthy of further investigation.

The likelihood of encountering threatening weather conditions at the end of a migratory flight may also be an important factor affecting migrant decisions (Nisbet and Drury 1968). The challenge of meeting energetic demands in cold or rainy weather might be exacerbated by the elevated numbers of migrants present in stopover habitats under such weather conditions, if the migrants compete with one another for food or other resources. The population-level impacts of this possibility may be ameliorated by generally higher fat reserves in migrants that stopover in inclement weather (Moore and Kerlinger 1987, Simons et al. 2004). More study is needed on the consequences of inclement weather on the ability to continue migration in good body condition.

ACKNOWLEDGMENTS

The authors thank the many homeowners of the study area who tolerated our presence in front of their house on so many mornings. The manuscript benefited from the comments of F. R. Moore and two anonymous reviewers.

LITERATURE CITED

Able, K. 1972. Fall migration in coastal Louisiana and the evolution of migration patterns in the Gulf Region. Wilson Bulletin 84:231–242.

Alerstam, T. 1990. Bird migration. Cambridge University Press, Cambridge, United Kingdom.

Berthold, P. 2001. Bird migration: a general survey. Second Edition. Oxford University Press, Oxford, United Kingdom.

Dennis, J. V. 1954. Meteorological analysis of occurrence of grounded migrants at Smith Point, Texas, April 17–May 17, 1951. Wilson Bulletin 66:102–111.

Duncan, R. A. 1994. Bird migration, weather, and fallout, including the migrant traps of Alabama and northwest Florida. Self-published, Gulf Breeze, Florida, USA.

Gauthreaux Jr., S. A. 1971. A radar and direct visual study of passerine spring migration in southern Louisiana. Auk 88:343–365.

Gauthreaux Jr., S. A., J. E. Michi, and C. Belser. 2005. The temporal and spatial structure of the atmosphere and its influence on bird migration strategies. Pages 182–193 *in* Birds of two worlds: the ecology and evolution of migration (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, Maryland, USA.

Lack, D. 1960. The influence of weather on passerine migration: a review. Auk 77:171–209.

Loria, D. E. and F. R. Moore. 1990. Energy demands of migration on Red-eyed Vireos (*Vireo olivaceous*). Behavioral Ecology 1:24–35.

Lowery Jr., G. H. 1945. Trans-Gulf spring migration of birds and the coastal hiatus. Wilson Bulletin 57: 92–121.

Moore, F. and P. Kerlinger. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47–54.

Muller, R. A. 1977. A synoptic climatology for environmental baseline analysis: New Orleans. Journal of Applied Meteorology 16:20–34.

Nisbet, I. C. T. and W. H. Drury Jr. 1968. Short-term effects of weather on bird migration: a field study using multivariate statistics. Animal Behaviour 16:496–530.

Richardson, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

Richardson, W. J. 1990. Timing of bird migration in relation to weather: updated review. Pages 79–101 *in* Bird migration: physiology and ecophysiology (E. Gwinner, Editor). Springer-Verlag, Berlin, Germany.

Simons, T. R., F. R. Moore, and S. A. Gauthreaux Jr. 2004. Mist-netting trans-Gulf migrants at coastal stopover sites: the influence of spatial and temporal variability on capture data. Studies in Avian Biology 29:135–143.

U.S. Department of Commerce. 1994–2000. Daily weather maps. Climate Prediction Center, Washington, D.C., USA.

Zar, J. H. 1984. Biostatistical analysis. Second Edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

The Wilson Journal of Ornithology 120(2):296–303, 2008

MASS CHANGES OF MIGRATORY LANDBIRDS DURING STOPOVERS IN A NEW YORK CITY PARK

CHAD L. SEEWAGEN[1,2,3] AND ERIC J. SLAYTON[1]

ABSTRACT.—We measured rates of mass change of eight species of migratory passerines in a New York City park during three consecutive spring and autumn migrations to evaluate the quality of an urban habitat as a stopover site. We also examined seasonal differences in body condition. Linear regressions of a condition index on time of day detected significant hourly mass gain by Magnolia Warbler (*Dendroica magnolia*), Black-throated Blue Warbler (*D. caerulescens*), Ovenbird (*Seiurus aurocapilla*), and Northern Waterthrush (*S. noveboracensis*) during spring, and Common Yellowthroat (*Geothlypis trichas*) during autumn. Swainson's Thrush (*Catharus ustulatus*) showed significant mass loss during autumn. Significant spring mass gain rates ranged from 0.99 to 2.46% of mean body mass/hr. Common Yellowthroat gained 1.28% of mean body mass/hr during autumn. Most species were heavier and fatter in spring than autumn. The significant mass gain rates were comparable to those in similar studies in more pristine areas. Our results suggest the urban stopover site we examined is a place where migrants can sufficiently replenish energy stores. This highlights the importance of conserving and properly managing remaining green spaces in urban areas along major migratory bird flyways. *Received 1 June 2007. Accepted 17 August 2007.*

Nearctic-neotropical migratory passerines engage in episodes of intense exercise during nocturnal migratory flights followed by periods of hyperphagia and rapid fat deposition during stopovers. Stopover habitats in which depleted energy stores can be promptly replenished are necessary for successful and timely migrations (Moore et al. 1995). The fate of birds during this stage of their life-cycle can limit population sizes (Sillett and Holmes 2002), and meeting the habitat requirements of migration has become a primary component of current migratory landbird conservation strategies (e.g., Dettmers and Rosenberg 2000).

Despite the rapidly growing interest over the last 20 years in stopover ecology (Moore and Kerlinger 1987, Woodrey and Moore 1997, Wang et al. 1998, Carlisle et al. 2005), stopover site quality (Russell et al. 1994; Dunn 2000, 2001; Rimmer and McFarland 2000), and stopover site conservation (McCann et al. 1993, Moore et al. 1995, Mehlman et al. 2005), migrant use of urban habitats has received little attention. The Atlantic Coast migration routes overlap with the most urbanized region of North America and the habitats remaining within cities may have an important role in landbird migration (Mehlman et al. 2005). However, it is unknown whether urban parks provide migrants with resources they need during stopovers. The high densities of birds, predominance of exotic invasive plants, and overall degraded habitat conditions often present in such areas may elevate competition for resources and constrain the ability of migrants to sufficiently refuel. City parks and similar habitat fragments will represent an increasing proportion of the stopover sites available to migrants as urbanization proceeds. Thus, the stopover ecology of birds in these areas is deserving of greater attention. Our objective was to measure the mass change of migrants during stopovers in Bronx Park, New York City, and gauge the quality of an urban habitat as a migratory bird stopover site. We also examined seasonal differences in body condition to learn if migrants carried greater fat loads in spring than autumn, as has often been observed in non-urban areas (e.g., Winker et al. 1992b, Morris and Glasgow 2001).

METHODS

Site Description.—Bronx County, New York, has a human population of ~1.4 million and a total land area of 109 km^2, equaling a population density of 12,844 people/km^2 (U.S. Census Bureau 2004). Bronx Park is a 229-ha municipal park at the center of the county. The park is composed almost entirely of the

[1] Department of Ornithology, Wildlife Conservation Society, Bronx, NY 10460, USA.

[2] Department of Biology, University of Western Ontario, London, ON N6A 5B7, Canada.

[3] Corresponding author;
e-mail: cseewagen@wcs.org

campuses of the Bronx Zoo and New York Botanical Garden. The Bronx River bisects Bronx Park before joining the East River to the south. Our study area was an approximately 4.9-ha section of riparian and upland forest on the grounds of the Bronx Zoo (40° 85′ N, 73° 87′ W). The site does not contain any animal exhibits and is not open to zoo visitors. The west side of this area is a mature dry upland deciduous forest dominated by red oak (*Quercus rubra*) and sweet gum (*Liquidambar styraciflua*) with some white ash (*Fraxinus americana*), mockernut (*Carya tomentosa*), black cherry (*Prunus serotina*), and American elm (*Ulmus americana*) also present. The upland forest transitions rapidly down a steep rocky gradient to the east into a riparian zone with wet or seasonally wet soils. The most common riparian species are willows (*Salix* spp.) and swamp dogwood (*Cornus foemina*). Two non-native invasive plants, Japanese knotweed (*Polygonum cuspidatum*) and Oriental bittersweet (*Celastrus orbiculatus*), are prevalent.

We note that urban habitats can vary considerably with regard to size, vegetation composition, extent of human use/recreation, historical and current management practices, abundance of birds using them as stopover sites, and other factors that may influence their quality as migratory bird stopover habitat. Therefore the birds captured in Bronx Park should not be considered representative of birds that use dramatically different types of habitats within cities during migration (e.g., Seewagen 2008).

Data Collection.—Birds were captured in 10–14 mist nets during spring and autumn of 2004–2006. Nets were operated from sunrise until ~ 1200 hrs EST, 5 days/week (weather permitting). Autumn sampling began on 4–6 September each year and ended on 17–18 October. Spring sampling began on 28 April–2 May and ended on 1–2 June. Nets were set in 10 locations (some nets were doubled) throughout the site and remained in place for the duration of the study. Six net locations were within close proximity to the river's edge (<10 m), while the remaining four locations were ~40 m from the river in the upland area.

Nets were checked approximately every 30 min. Captured birds were measured (tail and unflattened wing length in mm), classified to age and gender when possible (Pyle 1997), weighed to the nearest 0.1 g (Ohaus 400 g digital balance), and banded with federal metal bands. Visible subcutaneous fat in the furcular hollow was rated on a six-point scale (Moore and Kerlinger 1987). Fat was scored by the same observer throughout the study with the exception of 5 days during autumn 2004 and 2 days during autumn 2005 to minimize inter-observer variation (Krementz and Pendleton 1990).

Focal Species.—We selected eight focal species based on their sample sizes (>25 total individuals of each in spring and autumn) and a lack of large breeding or over-wintering populations in or near our study site: Swainson's Thrush (*Catharus ustulatus*), Wood Thrush (*Hylocichla mustelina*), Magnolia Warbler (*Dendroica magnolia*), Black-throated Blue Warbler (*D. caerulescens*), Yellow-rumped Warbler (*D. coronata*), Ovenbird (*Seiurus aurocapilla*), Northern Waterthrush (*S. noveboracensis*), and Common Yellowthroat (*Geothlypis trichas*). Common Yellowthroat and Yellow-rumped Warbler are exceptions to our criteria in that the former breeds locally and the latter often over-winters in nearby coastal areas (NYSBBA 2000; DeCandido and Allen 2005; CLS, pers. obs.). However, because sample sizes for both species were relatively large, we assumed the majority of individuals that we captured were transients. Only one Common Yellowthroat was recaptured more than 1 week following initial capture during spring, and no Yellow-rumped Warblers were recaptured during autumn suggesting the individuals in our samples did not remain in the study site to breed or over-winter. There were no between-season or between-year captures of Common Yellowthroats or Yellow-rumped Warblers, unlike individuals of other species that nested, over-wintered, or resided year-round in the study site during 2004–2006 (e.g., Warbling Vireo [*Vireo gilvus*], American Robin [*Turdus migratorius*], Gray Catbird [*Dumetella carolinensis*], Song Sparrow [*Melospiza melodia*], and Baltimore Oriole [*Icterus galbula*]).

Statistical Analyses.—We used Mann-Whitney *U*-tests to compare fat scores between seasons (Hailman 1965). Medians and means are both presented, as the median is the most appropriate measure of central tendency for

fat score data but the mean is more commonly reported in other studies (Hailman 1965, Benson and Winker 2005).

We calculated a condition index (mass × 100/wing length) to correct body mass for body size variation (Winker 1995, Dunn 2002, Bonter et al. 2007). We used *t*-tests to examine differences in condition indices (Carlisle et al. 2005) between seasons. We first tested the relationship between condition index and fat score in spring and autumn with Pearson's product-moment correlations because differences in body mass may not be entirely attributable to differences in fat content (Piersma 1990, Scott et al. 1994, Karasov and Pinshow 1998).

Simple linear regressions of condition index and time of day (converted to hours since sunrise at time of capture) were used to estimate hourly changes in condition (Morris et al. 1996; Dunn 2001, 2002; Carlisle et al. 2005; Bonter et al. 2007). Changes in condition were converted to changes in mass using the mean spring and autumn wing lengths for each species. We first regressed wing length on time of day to reveal any existing temporal biases in body size that might distort mass change estimates when using this method (Winker 1995).

Statistical tests were performed with SYSTAT, Version 10.0 (Systat Software Inc. 2000), and PRISM, Version 4.0 (GraphPad Software Inc. 2005) software packages. We considered results statistically significant when $P \leq 0.05$.

RESULTS

Capture Rates and Species Richness.—Our sampling effort totaled 2,599 net hrs in spring and 3,764 in autumn. The average spring capture rate of Nearctic-neotropical species (n = 49) equaled 53.9 birds/100 net hrs; the average spring capture rate of all species (n = 63) equaled 59.5 birds/100 net hrs. Nearctic-neotropical species (n = 48) were captured during autumn at an average rate of 37.3 birds/100 net hrs and all species (n = 70) were captured at an average rate of 49.8 birds/100 net hrs.

Fat Score and Condition Index.—Condition indices were significantly correlated with fat scores in each species in both seasons (Pearson's product-moment correlation tests, all $P < 0.001$) suggesting that differences in condition indices reflected differences in lipid stores. Fat scores and condition indices were higher in spring than autumn for Black-throated Blue Warbler, Common Yellowthroat, Magnolia Warbler, and Yellow-rumped Warbler (all $P < 0.005$; Table 1). Swainson's Thrushes had higher fat scores in spring than autumn, but showed no seasonal difference in condition indices. Fat scores for Northern Waterthrush did not differ between seasons and condition indices were higher in spring than autumn. Wood Thrush was the only species for which fat scores and condition indices were higher in autumn than spring (Table 1).

Rate of Mass Change.—Linear regressions of wing length on time of day were negative for Yellow-rumped Warbler during spring and autumn (spring: $r^2 = 0.03$, $P = 0.020$; autumn: $r^2 = 0.04$, $P = 0.027$) and Swainson's Thrush during autumn ($r^2 = 0.22$, $P = 0.011$). No other species showed significant interactions between body size and time of day.

The relationship between condition index and time of day was significant in six (all $P < 0.05$), and nearly significant in one ($P = 0.067$) of 16 combinations of species and season. Slopes were positive in six of these seven regressions. During spring, Magnolia Warbler, Black-throated Blue Warbler, Ovenbird, and Northern Waterthrush showed significant mass gains, ranging from 0.99 to 2.46% of mean body mass/hr. Common Yellowthroat gained 1.28%/hr during autumn. Swainson's Thrush in autumn was the only species to lose significant mass (−4.46%/hr; Table 2). Swainson's Thrush was the only species for which spring and autumn mass change rates differed ($F_{1,78} = 8.80$, $P = 0.004$). However, linear regressions were not significant for any species in both seasons, preventing meaningful comparisons of mass change rates among spring and autumn.

DISCUSSION

Fat Score and Condition Index.—Most of the species we examined were heavier and fatter in spring than autumn, similar to another recent study in New York City (Seewagen 2008). These results are consistent with findings in non-urban areas (e.g., King et al. 1963, Winker et al. 1992b, Morris and Glasgow 2001, Dunn 2002, but see Benson and Winker 2005). Greater fat loads during spring are be-

TABLE 1. Seasonal differences in condition indices (mass × 100/wing length, *t*-test) and fat scores (Mann-Whitney *U*-test) of migratory landbirds during stopovers in Bronx Park, New York City, 2004-2006. Values are mean ± SD; fat score medians presented in parentheses.

Species	Season	*n*	Condition	*t*	*P*	Fat score	*Z*	*P*
Swainson's Thrush	Spring	53	0.339 ± 0.032	0.7	0.489	2.4 ± 1.3 (2)	2.83	0.005
	Autumn	29	0.334 ± 0.043			1.5 ± 1.6 (1)		
Wood Thrush	Spring	34	0.478 ± 0.029	5.9	<0.001	1.1 ± 0.9 (3)	3.78	<0.001
	Autumn	33	0.540 ± 0.053			2.6 ± 1.6 (1)		
Magnolia Warbler	Spring	28	0.163 ± 0.013	10.3	<0.001	3.5 ± 1.1 (4)	6.42	<0.001
	Autumn	76	0.141 ± 0.009			1.6 ± 1.1 (1)		
Black-throated Blue Warbler	Spring	30	0.175 ± 0.010	7.37	<0.001	3.1 ± 1.4 (3)	4.84	<0.001
	Autumn	62	0.154 ± 0.014			1.3 ± 1.5 (1)		
Yellow-rumped Warbler	Spring	194	0.192 ± 0.015	16.82	<0.001	3.2 ± 1.1 (3)	11.40	<0.001
	Autumn	132	0.165 ± 0.012			1.2 ± 1.2 (1)		
Ovenbird	Spring	110	0.274 ± 0.019	0.59	0.559	2.2 ± 1.2 (2)	1.93	0.054
	Autumn	40	0.271 ± 0.025			1.8 ± 1.7 (1)		
Northern Waterthrush	Spring	138	0.239 ± 0.022	2.3	0.022	2.4 ± 1.4 (2)	1.80	0.072
	Autumn	71	0.231 ± 0.024			2.0 ± 1.5 (2)		
Common Yellowthroat	Spring	128	0.200 ± 0.016	5.66	<0.001	2.9 ± 1.5 (3)	4.92	<0.001
	Autumn	147	0.189 ± 0.015			1.9 ± 1.6 (2)		

TABLE 2. Estimated hourly mass changes of migratory landbirds during stopovers in Bronx Park, New York City, 2004–2006. Mass change rates are based on linear regressions of condition index (mass × 100/wing length) and hours since sunrise at time of capture.

Species	Season	*n*	Wing (mm)	Mass (g)	*r*	*F*	df	*P*	g/hr	% mean mass/hr
Swainson's Thrush	Spring	53	97	33.1	0.15	1.18	1,51	0.283	0.29	0.87
	Autumn	29	97	32.3	0.43	6.25	1,27	0.019	−1.44	−4.46
Wood Thrush	Spring	34	105	50.1	0.02	0.02	1,32	0.893	−0.05	−0.09
	Autumn	31	105	56.8	0.08	0.53	1,29	0.471	0.50	0.87
Magnolia Warbler	Spring	28	58	9.5	0.51	9.27	1,26	0.005	0.24	2.46
	Autumn	76	59	8.3	0.18	2.53	1,74	0.116	0.07	0.88
Black-throated Blue Warbler	Spring	30	62	10.8	0.39	5.12	1,28	0.032	0.20	1.86
	Autumn	62	63	9.6	0.01	0.00	1,60	0.969	0.00	0.00
Yellow-rumped Warbler	Spring	195	71	13.6	0.08	1.13	1,193	0.288	0.06	0.43
	Autumn	132	70	11.6	0.16	3.40	1,130	0.067	0.14	1.20
Ovenbird	Spring	110	74	20.2	0.24	6.53	1,108	0.012	0.22	1.11
	Autumn	40	74	20.1	0.08	0.26	1,38	0.613	0.12	0.62
Northern Waterthrush	Spring	138	75	17.8	0.17	3.98	1,136	0.048	0.18	0.99
	Autumn	71	75	17.3	0.01	0.01	1,69	0.916	0.02	0.11
Common Yellowthroat	Spring	126	54	10.7	0.00	0.00	1,124	0.967	0.00	0.00
	Autumn	147	54	10.2	0.19	5.54	1,145	0.020	0.13	1.28

TABLE 3. Hourly mass changes of migratory landbirds at urban and non-urban stopover sites. Rates from previous studies are based on linear regressions of body mass or size-corrected body mass on time of day. Some original values from other studies were converted to g/hr or % mass/hr to allow for closer comparison with the results of this study.

Species	Season	Minnesota[a] (g)	Minnesota[b] (g)	Ontario[c] (%)	Ontario[d] (g)	New York State[e] (%)	This study g (%)
Swainson's Thrush	Autumn		0.20	0.21	0.02	0.41	−1.44 (−4.46)
Magnolia Warbler	Spring			0.82		0.41	0.235 (2.46)
Black-throated Blue Warbler	Spring			1.02		0.52	0.20 (1.86)
Ovenbird	Spring	0.11		0.38			0.22 (1.11)
Northern Waterthrush	Spring		0.17				0.18 (0.99)
Common Yellowthroat	Autumn	0.10		1.01	0.00	1.58	0.13 (1.28)

[a] Table 3 in Winker et al. 1992a. Gross Δg/day divided by 12 hrs to convert rate to hourly mass change.
[b] Table 6 in Winker et al. 1992b. Gross Δg/day divided by 12 hrs to convert rate to hourly mass change.
[c] Table 1 in Dunn 2001. Values are expressed as % lean mass. The highest significant rate among the three study sites for each species is presented.
[d] Table 1 in Jones et al. 2002. Rates are presented as the average of the hatching-year and after-hatching year rates.
[e] Table 1 and 2 in Bonter et al. 2007. Values are expressed as % lean mass.

lieved to provide subsequent reproductive benefits upon arrival in breeding areas (Sandberg and Moore 1996, Smith and Moore 2003). The trend we observed may also be a result of autumn migrants not depositing large fat stores until further south of our site (Winker et al. 1992b).

Rate of Mass Change.—The ability to replenish depleted fat stores may be the greatest constraint birds have during migration (Moore et al. 1995), and the rate at which migrants gain mass during stopovers is a commonly used indicator of habitat quality (Dunn 2000, 2001; Bonter et al. 2007). Six of the seven significant or marginally significant interactions between condition and time of day were positive in our study indicating the study site is stopover habitat in which migrants can gain body mass. Moreover, negative relationships were in the minority (2 of 16), and only one was statistically significant. The extreme rate of mass loss predicted by linear regression in Swainson's Thrush during autumn may be a consequence of small sample size and the method's assumption that birds arrive at the site at or prior to dawn on the day of capture (Dunn 2000, Jones et al. 2002). Swainson's Thrushes with extremely high condition indices (and fat scores of 5) were captured shortly after sunrise on two occasions, strongly influencing the slope of the regression line. It is unlikely these individuals just arrived in the study site as the regression method assumes. Additionally, Swainson's Thrush body size during autumn was significantly correlated with time of day, in which case the regression method is likely to produce a misleading estimate (Winker 1995).

Some mass gain rates measured in this study exceed those from less disturbed, non-urban areas (Table 3) and suggest ample resources are available to migrants in Bronx Park. Urban ecosystems often support higher densities of arthropods than non-urban habitats (Kahn and Cornell 1989, Hanks and Denno 1993, reviewed by McIntyre 2000) and, in turn, potentially provide plentiful food sources for insectivorous migrants. Increased densities of arthropods in urban habitats have been attributed to several factors, including warmer microclimates that result from the "urban heat island effect". We speculate that another potential benefit of the urban heat island effect to migrants is a reduction in over-night thermoregulation costs. Warmer temperatures at night in urban habitats might permit greater net energy gains than are possible in cooler non-urban areas (see Wikelski et al. 2003). Migrants at our study site may be advantaged by the relative absence of predators (e.g., small-bodied diurnal raptors; CLS and EJS, pers. obs.) compared to larger, more pristine areas. A lack of predators might allow for uninhibited foraging intensity relative to situations where migrants need to be concerned with predator avoidance (Cimprich et al. 2005). We recommend that future studies of urban stopover ecology investigate these topics in concert with measurements of migrant mass change rates.

City parks often represent the only stopover habitat available to migrants encountering

North America's vast metropolitan areas. It is therefore important to learn whether these areas are providing migrants with resources they need. This study provides evidence of migrants gaining body mass through the morning hours in Bronx Park, suggesting that an urban habitat is serving as a suitable stopover site. It also highlights the need to conserve and properly manage the green spaces remaining within cities along major flyways.

Our findings cannot be generalized across all urban habitats because of great variation in intrinsic characteristics that likely influence site quality. We encourage further research in a diversity of urban areas to more comprehensively understand the stopover ecology of migratory birds in urban habitats.

ACKNOWLEDGMENTS

This research was funded by the Wildlife Conservation Society with additional support from the Nuttall Ornithological Club. We dedicate this paper to Georges Dremeaux, who knew the birds of Bronx Park perhaps better than anyone. We thank Marcia Arland, A. J. Bernick, Marshal Case, N. J. Clum, Sharon Kass, G. J. Russell, C. D. Sheppard, and A. M. Torregrossa for valuable advice, assistance, and contributions throughout the project. Our manuscript benefited from reviews by J. D. Carlisle and Robert DeCandido. Librarians Robert Olley and Steve Johnson acquired literature for this study. We thank the many people who continuously encouraged us to pursue this research: George Amato, James Breheny, R. A. Cook, William Conway, Robert DeCandido, K. A. Hatch, Yula Kapetanakos, Paul Kerlinger, M. W. Klemens, Richard Lattis, Nick Miller, J. W. Rowden, E. W. Sanderson, and W. A. Weber. We also thank Deborah Allen, Peter Clyne, Katie Hine, Karen Jasper, Florence Klecha, Coby Klein, Mary Iorizzo, Adriana Palmer, Jean Rothe, Emily Stevenson, Brian Tierney, and the many others who assisted us in the field.

LITERATURE CITED

Benson, A. M. and K. Winker. 2005. Fat deposition strategies among high-latitude passerine migrants. Auk 122:544–557.

Bonter, D. N., T. M. Donovan, and E. W. Brooks. 2007. Daily mass changes in landbirds during migration stopover on the south shore of Lake Ontario. Auk 124:122–133.

Carlisle, J. D., G. S. Kaltenecker, and D. L. Swanson. 2005. Stopover ecology of autumn landbird migrants in the Boise foothills of southwestern Idaho. Condor 107:244–258.

Cimprich, D. A., M. S. Woodrey, and F. R. Moore. 2005. Passerine migrants respond to variation in predation risk during stopover. Animal Behavior 69:1173–1179.

DeCandido, R. and D. Allen. 2005. First confirmed nesting of the Pine Warbler (*Dendroica pinus*) in New York City. Kingbird 55:328–334.

Dettmers, R. and K. V. Rosenberg. 2000. Partners in Flight Landbird Conservation Plan: Physiographic Area 9: Southern New England. Version 1.0. American Bird Conservancy, The Plains, Virginia, USA.

Dunn, E. H. 2000. Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. Auk 117:12–21.

Dunn, E. H. 2001. Mass change during migration stopover: a comparison of species groups and sites. Journal of Field Ornithology 72:419–432.

Dunn, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson Bulletin 114:368–379.

GraphPad Software Inc. 2005. PRISM Version 4.0. GraphPad Software Inc., San Diego, California, USA.

Hailman, J. P. 1965. Notes on quantitative treatments of subcutaneous lipid data. Bird-Banding 36:14–20.

Hanks, L. M. and R. F. Denno. 1993. Natural enemies and plant water relations influence the distribution of an armored scale insect. Ecology 74:1081–1091.

Jones, J., C. M. Francis, M. Drew, S. Fuller, and M. W. S. Ng. 2002. Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. Condor 104: 49–58.

Kahn, D. M. and H. V. Cornell. 1989. Leafminers, early leaf abscission, and parasitoids: a tritrophic interaction. Ecology 70:1219–1226.

Karasov, W. H. and B. Pinshow. 1998. Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71:435–448.

King, J. R., S. Barker, and D. S. Farner. 1963. A comparison of energy reserves during autumnal and vernal migratory periods in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. Ecology 44:513–521.

Krementz, D. G. and G. W. Pendleton. 1990. Fat scoring: sources of variability. Condor 92:500–507.

McCann, J. M., S. E. Mabey, L. J. Niles, C. Bartlett, and P. Kerlinger. 1993. A regional study of coastal migratory stopover habitat for neotropical migrant songbirds: land management implications. Transactions of the North American Wildlife and Natural Resources Conference 58:398–407.

McIntyre, N. E. 2000. Ecology of urban arthropods: a review and a call to action. Annals of the Entomological Society of America 93:825–835.

Mehlman, D. W., S. E. Mabey, D. N. Ewert, C. Duncan, B. Abel, D. Cimprich, R. D. Sutter, and M. Woodrey. 2005. Conserving stopover sites for

forest-dwelling migratory landbirds. Auk 122: 1281–1290.

Moore, F. R. and P. Kerlinger. 1987. Stopover and fat deposition by North American wood-warblers following spring migration over the Gulf of Mexico. Oecologia 74:47–54.

Moore, F. R., S. A. Gauthreaux, P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121–144 *in* Ecology and management of neotropical migratory birds: a synthesis and review of critical issues (T. E. Martin and D. M. Finch, Editors). Oxford University Press, New York, USA.

Morris, S. R. and J. L. Glasgow. 2001. Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. Wilson Bulletin 113: 202–210.

Morris, S. R., D. W. Holmes, and M. E. Richmond. 1996. A ten year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. Condor 98:395–408.

New York State Breeding Bird Atlas (NYSBBA). 2000. Atlas results. http://www.dec.state.ny.us/website/dfwmr/wildlife/bba/index.html (accessed 4 August 2006).

Piersma, T. 1990. Pre-migratory "fattening" usually involves more than the deposition of fat alone. Ringing and Migration 11:113–115.

Pyle, P. 1997. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, California, USA.

Rimmer, C. C. and K. P. McFarland. 2000. Migrant stopover and postfledgling dispersal at a montane forest site in Vermont. Wilson Bulletin 112:124–136.

Russell, R. W., F. L. Carpenter, M. A. Hixon, and D. C. Paton. 1994. The impact of variation in stopover habitat quality on migrant Rufous Hummingbirds. Conservation Biology 8:483–490.

Sandberg, R. and F. R. Moore. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. Oikos 77:577–581.

Scott, I., P. I. Mitchell, and P. R. Evans. 1994. Seasonal changes in body mass, body composition and food requirements in wild migratory birds. Proceedings of the Nutrition Society 53:521–531.

Seewagen, C. L. 2008. Lipid content of Nearctic-neotropical migratory passerines killed during stopovers in a New York City park. Northeastern Naturalist 15:87–96.

Sillett, T. S. and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71: 296–308.

Smith, R. J. and F. R. Moore. 2003. Arrival fat and reproductive performance in a long distance passerine migrant. Oecologia 134:325–331.

Systat Software Inc. 2000. SYSTAT Version 10.0. Systat Software Inc., San Jose, California, USA.

U.S. Census Bureau. 2004. State and county quick facts. http://quickfacts.census.gov/qfd/states/36/36005.html (accessed 8 December 2005).

Wang, Y., D. Finch, F. R. Moore, and J. F. Kelly. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. Auk 115:829–84.

Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. Henk Visser. 2003. Costs of migration in free-flying songbirds. Nature 423: 704.

Winker, K. 1995. Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic-Neotropic migrants. Auk 112:690–700.

Winker, K., D. W. Warner, and A. R. Weisbrod. 1992a. Daily mass gains among woodland migrants at an inland stopover site. Auk 109:853–862.

Winker, K., D. W. Warner, and A. R. Weisbrod. 1992b. The Northern Waterthrush and Swainson's Thrush as transients at a temperate inland stopover site. Pages 384–402 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagen III and D. W. Johnston, Editors). Manomet Bird Observatory, Manomet, Massachusetts and Smithsonian Institution Press, Washington D.C., USA.

Woodrey, M. S. and F. R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. Auk 114:695–707.

The Wilson Journal of Ornithology 120(2):304–310, 2008

MIGRATION OF FLORIDA SUB-ADULT BALD EAGLES

ELIZABETH K. MOJICA,[1,5,7] J. MICHAEL MEYERS,[2] BRIAN A. MILLSAP,[3,6] AND KATHERIN L. HALEY[4]

ABSTRACT.—We used satellite telemetry locations accurate within 1 km to identify migration routes and stopover sites of 54 migratory sub-adult Bald Eagles (*Haliaeetus leucocephalus*) hatched in Florida from 1997 to 2001. We measured number of days traveled during migration, path of migration, stopover time and locations, and distance traveled to and from winter and summer areas for each eagle (1–5 years old). Eagles used both Coastal Plain (n = 24) and Appalachian Mountain (n = 26) routes on their first migration north. Mountain migrants traveled farther ($\bar{x}$ = 2,112 km; 95% CI: 1,815–2,410) than coastal migrants ($\bar{x}$ = 1,397 km; 95% CI: 1,087–1,706). Eagles changed between migration routes less often on northbound and southbound movements as they matured (χ^2 = 13.22, df = 2, $P < 0.001$). One-year-old eagles changed routes between yearly spring and fall migrations 57% of the time, 2-year-olds 30%, and 3–5-year-olds changed only 17% of the time. About half (n = 25, 46%) used stopovers during migration and stayed 6–31 days ($\bar{x}$ = 14.8 days; 95% CI: 12.8–16.8). We recommend that migratory stopover site locations be added to GIS data bases for improving conservation of Bald Eagles in the eastern United States. *Received 18 May 2007. Accepted 20 September 2007.*

Migration of Bald Eagles (*Haliaeetus leucocephalus*) has been studied with some success using band recoveries and VHF radiotransmitters (Harmata et al. 1985, Hunt et al. 1992, McClelland et al. 1994, Wood and Collopy 1994, Harmata 2002). Using these methods, biologists found that eagles in Florida were partial migrants, i.e., sub-adults migrated north in summer, but many adults remained year-round residents (Broley 1947, Wood and Collopy 1994). Band recoveries indicated that Florida eagles migrate as far north as Prince Edward Island, Canada in summer and returned to Florida in winter (Broley 1947, Wood and Collopy 1994). Technological problems with tracking migration, and the cost of equipment and person-hours to follow eagles prevented a complete record of their long-distance movements, timing of their migration, and use of important migratory stopover sites. Recent improvements in tracking wildlife using satellite telemetry allows biologists to collect regular, less biased locations of migrating species over large areas (e.g., Millsap et al. 2004, Steenhof et al. 2005). This information could be valuable for the continued recovery and conservation of Bald Eagles in the continental United States. Our objectives were to: (1) document migration pathways, (2) identify timing, and (3) locate stopover sites of Florida sub-adult Bald Eagles in eastern North America using satellite telemetry.

METHODS

We attached 113-g platform terminal transmitter (PTT) packages to Bald Eagle nestlings (n = 69) reared in southwestern Florida during 1997–2001. Nestlings <10 weeks of age (1 per nest) were randomly selected from a subsample of rural and urban nests. We followed migration during 1997–2004 using satellite telemetry locations collected for 12 hrs approximately every 7 days to extend transmitter life to 4–5 years. We tested satellite telemetry accuracy using known locations of nestling eagles prior to fledging and extracted locations for use in analyses with accuracy within 1 km (Millsap et al. 2004). We excluded from our analyses 4 eagles because of PTT failure, 6 from mortalities, and 5 because they did not migrate outside Florida of the initial 69 eagles. We classified all eagles ages 0–5 as subadults. Eagles age 0–1 (juveniles) were categorized as first-year birds, ages 1–2 as

[1] Warnell School of Forestry and Natural Resources, The University of Georgia, Athens, GA 30602, USA.

[2] USGS, Patuxent Wildlife Research Center, Warnell School of Forestry and Natural Resources, The University of Georgia, Athens, GA 30602, USA.

[3] USDI, Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, VA 22203, USA.

[4] Florida Fish and Wildlife Conservation Commission, Division of Habitat and Species Conservation, Tallahassee, FL 32399, USA.

[5] Current address: Center for Conservation Biology, College of William and Mary, P. O. Box 8795, Williamsburg, VA 23187, USA.

[6] Current address: USDI, Fish and Wildlife Service, Albuquerque, NM 87102, USA.

[7] Corresponding author; e-mail: ekmojica@wm.edu

second-year birds, and ages 2–4 as 3–5-year old birds.

We estimated number of days eagles traveled during each spring and fall migration using their dates of departure and arrival. We estimated departure date as the median date from satellite transmissions before and after an eagle began continuous directional movement north or south. We did not use data if the interval between satellite transmissions was >2.5 weeks. We set the 2.5 week interval because it allowed us to include eagles in the analysis when satellite data were irregular or inaccurate during onset of migration. We assigned the arrival date by using the first day the eagle stopped directional movement and began a period of localized movements (<100 km radius) for >31 days. Eagles could have arrived up to 6 days earlier because of satellite transmission intervals. We separated spring migration data for first-year (juvenile) eagles because migration initiation of recently fledged eagles can be delayed compared to older sub-adults (Gerrard et al. 1978). There was no difference in fall migration date among age classes and data were pooled. We compared differences between the number of days traveled for first-year eagles during north and south migration by a paired comparison *t*-test (n = 40, Sokal and Rohlf 1995).

We delineated migration flyways using unfiltered satellite data to define general routes taken by first-year eagles. The small sample size of second through fifth-year eagles did not allow analysis of movements of older eagles. We plotted satellite locations during migration in ArcView 3.2 (ESRI 1999) with an Albers Equal Area Conic projection and connected locations on a map of eastern North America. We categorized migration routes by proximity to the Appalachian Mountains, i.e., any movements within the mountain boundary (Sure!Maps Raster 1995) were classified as mountain and routes east of the mountains were classified as coastal. We compared the changes between mountain and coastal routes to examine route fidelity for an individual by age class (1 year, 2 year, 3–5 year) using a Chi-square test (Sokal and Rohlf 1995). The Mississippi River Valley flyway was not included because of low sample size. We calculated distance traveled during migration by adding the linear distances by locations between winter and summer areas for each eagle. We compared migration distance between routes, by gender, and calendar year using three-way ANOVA (SAS Institute Inc. 1999).

We defined a stopover site as an area where an eagle made localized movements for 1 to 4 weeks during migration using two or more locations. We recorded the closest body of water using United States and Canadian hydrology data layers in ArcView (Natural Resources Canada 2001, USGS 2003). We measured the distance between stopover sites and estimated number of days spent at stopovers for each eagle. We averaged the distance traveled between stopovers if an eagle used multiple stopovers. We used one-way ANOVA to compare distance traveled between their first northbound and southbound migrations. Stopover site locations and durations are approximations because of gaps in data between scheduled satellite transmissions.

RESULTS

Recently fledged Bald Eagles began their first migration from April to June ($\bar{x} \pm$ SE = 30 May ± 3 days, median = 24 May, n = 52). Older sub-adults began migrating north from Florida earlier in spring, from late March to August ($\bar{x} \pm$ SE = 1 May ± 4 days, median = 30 Apr, n = 36). The return trip south began in late July–late December for all age classes ($\bar{x} \pm$ SE = 17 Sep ± 3 days, median = 21 Sep, n = 43, Fig. 1). The number of days eagles traveled on the first migration was greater for southbound than for northbound (paired *t*-test, $\bar{x}$ difference = 11 days, df = 38, t = 2.2, P = 0.032).

Eagles migrated north along the Coastal Plain (n = 24) and Appalachian Mountain (n = 26) routes during their first year (Fig. 2). Two eagles used the lower Mississippi River Valley to migrate to Mississippi and Missouri. Eagles changed their migration routes less on northbound and southbound movements as they became older (χ^2 = 13.7, df = 2, P < 0.001). One-year-old eagles changed routes between yearly spring and fall migrations 57% of the time, 2-year-olds 30%, and 3–5-year-olds changed only 17% of the time.

We found no difference for migratory distance traveled by gender ($F_{1,31}$ = 0.86, P = 0.36), year ($F_{3,31}$ = 0.25, P = 0.86) or their interaction terms. Route distances, however,

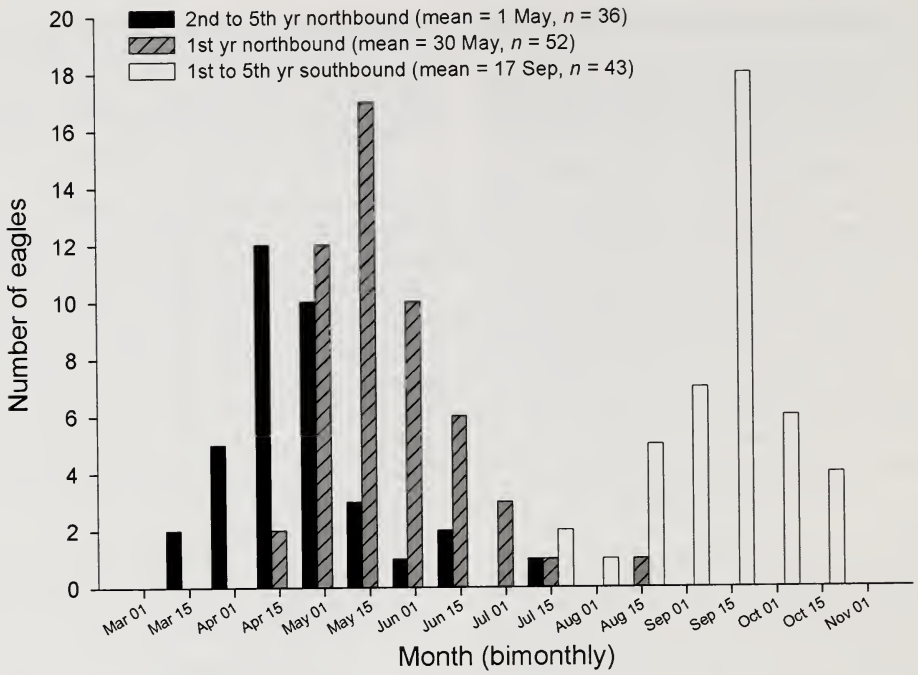


FIG. 1. Initiation dates of northbound and southbound migration for sub-adult Bald Eagles showing late departure of first-year eagles from Florida, 1997–2004. Dates calculated as means for individual Bald Eagles (*n*) using the number of years they survived.

did differ. Coastal migrants traveled less ($\bar{x}$ = 1,397 km) than mountain migrants ($\bar{x}$ = 2,112 km, $F_{1,31}$ = 9.11, P = 0.005). One eagle spent the summer 4,146 km north of Florida in coastal Labrador, Canada (51° N) and another visited NW Labrador at 55° N. Another eagle traveled only 340 km north of Florida and spent the summer on Lake Marion, South Carolina (33° N).

We documented 25 of 54 (46%) eagles using migratory stopovers. Eagles used stopovers 1–3 times during migration, staying 1–4 weeks ($\bar{x}$ = 14.8 days, median = 14 days, 95% CI: 12.8–16.8, n = 54, Fig. 3). All but one stopover duration was ≤31 days. One female spent the summer in New York and, during the first migration south, remained at a West Virginia stopover for 54 days, before continuing south to Florida. Mean distance traveled between stops on an eagle's first migration north ($\bar{x}$ = 1,405 km; 95% CI: 901–1,908; n = 9) was greater than their first migration south ($\bar{x}$ = 779 km; 95% CI: 402–1,156; n = 16; one-way ANOVA $F_{1,23}$ = 4.23, P = 0.051). We detected 20 northbound and 26 southbound stopover sites. Only one northbound stopover at Caledon State Park on the Potomac River was detected as a stopover during southbound migration.

DISCUSSION

Bald Eagles migrate in fall and spring to exploit seasonally available food, and to avoid areas where food becomes unavailable. Eagles feed primarily on exothermic fish near the surface that are sensitized to seasonal temperature fluctuations (Gerrard and Bortolotti 1988). Eagles in Florida are thought to migrate to higher latitudes in summer to escape high temperatures and to forage in areas with increased prey (Wood et al. 1998). The average fall and spring migration dates in this study correspond to previous reports from banding stations and telemetry studies (Broley 1947, Buehler et al. 1991, Weidensaul 2000). Wide variation in both departure and return dates suggests that migration behavior may not be attributed solely to prey abundance or air temperature.

We found undescribed migratory routes of Bald Eagles along the Appalachian Mountains and Mississippi Valley. Earlier studies in

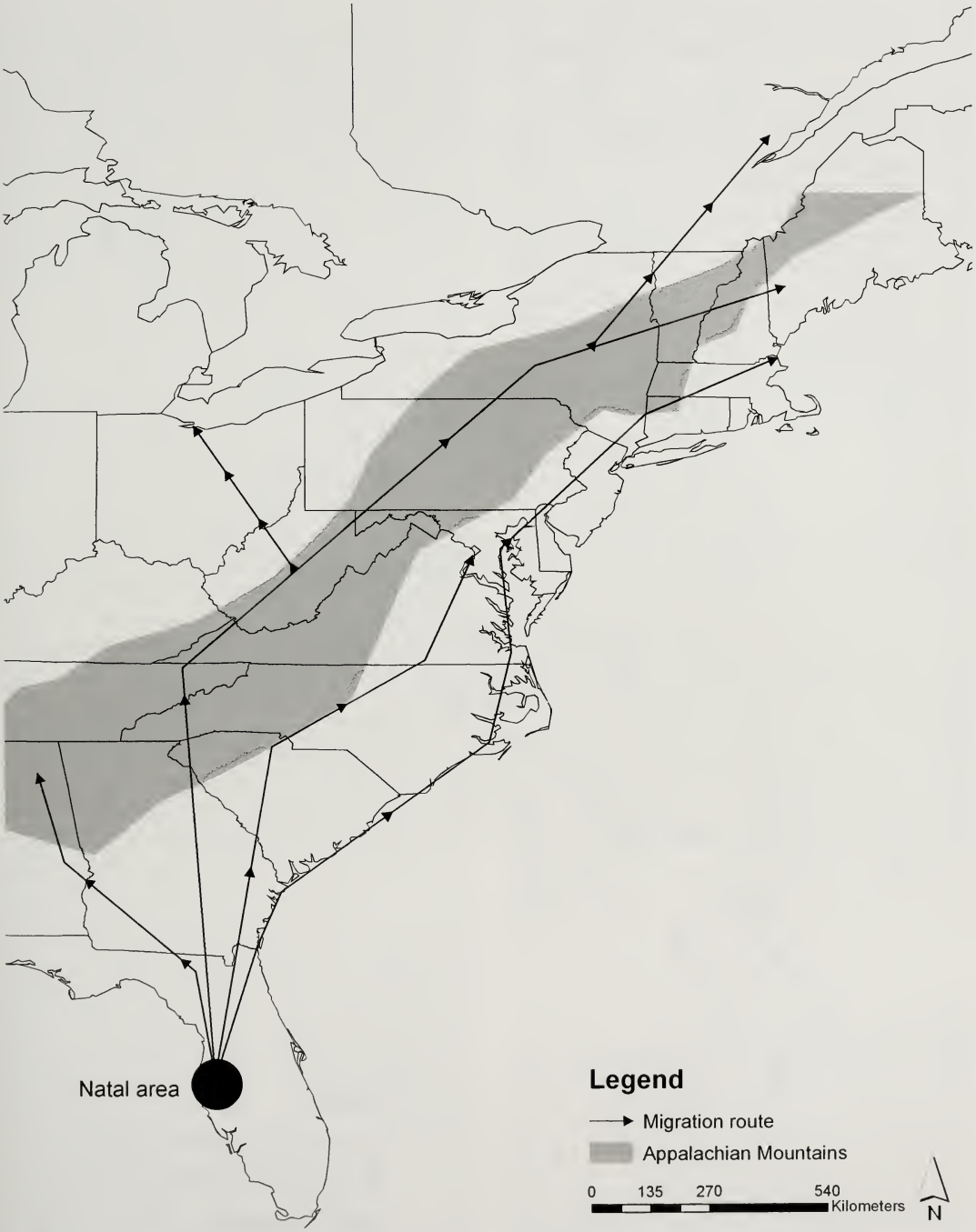


FIG. 2. Migration routes of sub-adult Bald Eagles (n = 54) hatched in Florida along the Appalachian Mountains (n = 26), Coastal Plain (n = 24), and Mississippi Valley (n = 2) in eastern North America, 1997–2004. Return routes southbound are similar to northbound routes shown by directional arrows. Eight of 69 sub-adult eagles did not migrate from Florida.

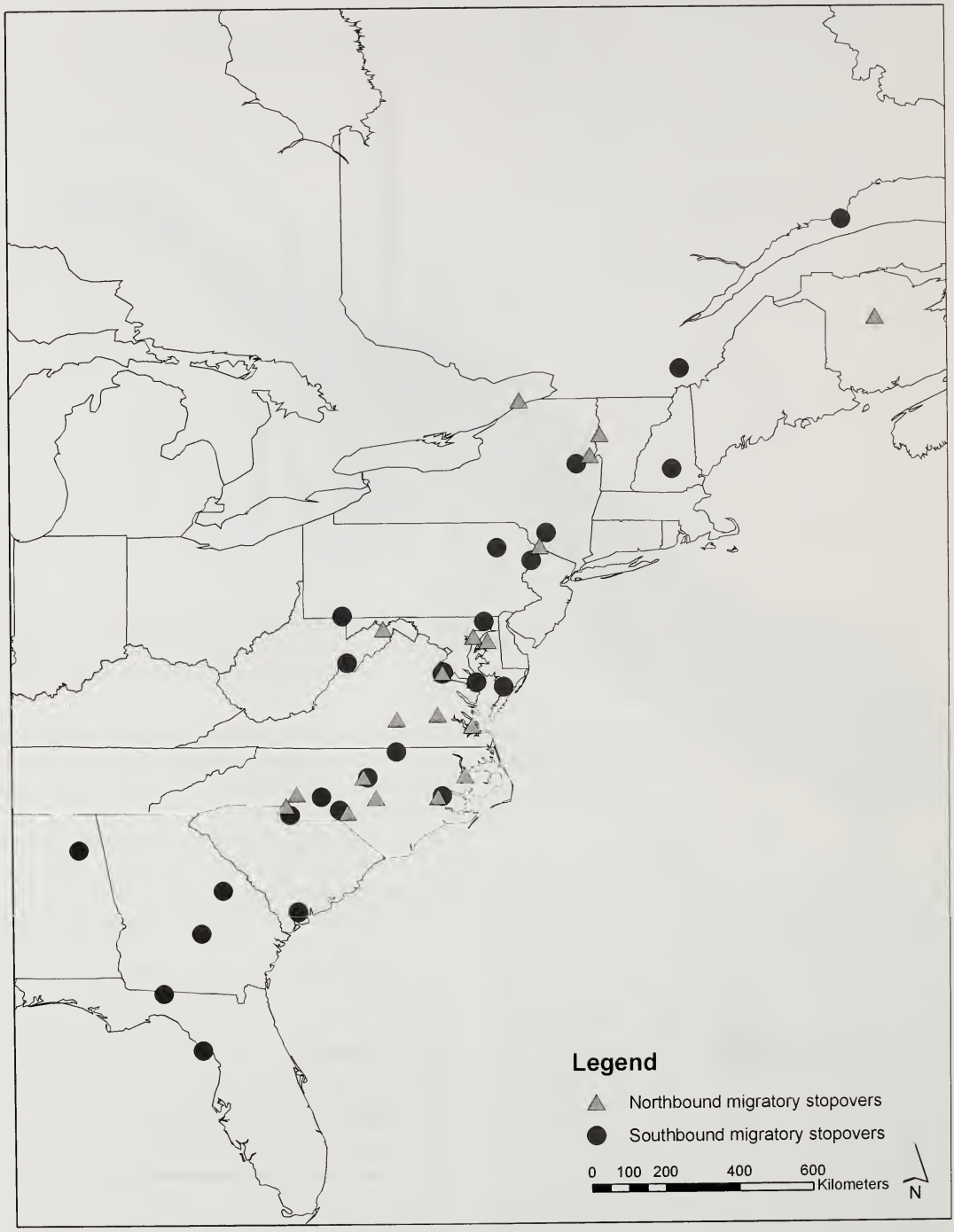


FIG. 3. Stopover sites used by sub-adult Bald Eagles (n = 25, ages 1–4) from Florida during northbound and southbound migration in eastern North America, 1997–2004.

southwest and north central Florida indicated that eagles used coastal routes predominantly (Broley 1947, Wood and Collopy 1994); however, we found equal use of coastal and mountain routes. Both males and females, and all sub-adult age classes used these migratory routes. We suspect that route choice may depend on prevailing winds at time of migration, location of natal areas, or genetic pre-programming (Broley 1947; Hunt et al. 1992; M. W. Collopy, pers. comm.). Biologists in the 1940s hypothesized that Florida eagles found in midwestern states in summer used the Mississippi Valley during migration (Broley 1947). Two eagles (4%) in this study used the Mississippi Valley flyway, but only the lower portion of that flyway. One female spent two consecutive summers in southern Illinois on the Mississippi River and winters in the Florida panhandle. Another female spent four summers in northeastern Alabama and southern Tennessee, and winters in west-central Florida. In addition, a male migrated north along the Appalachian Mountains before moving west to spend >1 summer on Lake Erie. The Coastal Plain, Appalachian Mountain, and Mississippi River migratory routes we describe may be specific to Florida Bald Eagles. An increase in route fidelity as eagles age suggests that young eagles learn to migrate efficiently. As an eagle gains more experience, it may seek the same stopover sites on a particular route.

We recorded migration distances >1,000 km farther than those reported in previous studies of Bald Eagles (range: 1,450–3,032 km; Grubb et al. 1994, McClelland et al. 1994, Wood and Collopy 1994). We attribute this to the ability to follow PTT-equipped eagles into remote areas of Canada >4,000 km from Florida. Two eagles, however, stopped their northern migration in Georgia and South Carolina, while the remaining eagles traveled several thousand additional kilometers. Some of the difference in distance traveled can be explained by migration routes, because coastal migrants traveled less distance overall than mountain migrants. We hypothesize that migrants using the mountain route may be able to travel farther by soaring in and gliding from abundant updrafts that are not found in the Coastal Plain (Heintzelman 1975, Hunt et al. 1992). In addition, the Chesapeake Bay region may serve to short-stop coastal migrants with abundant food resources and concentrations of other eagles.

Stopover sites may be important areas along migration routes where most eagles spend 1–4 weeks replenishing energy reserves. The estimated time spent at stopovers in this study was consistent with previous studies of hatching year sub-adults ($\bar{x}$= 14.5, range 1–25 days; Restani 2000, Laing et al. 2005). The small percentage of overlap between north and south stopover sites may indicate variation in migration resulting from seasonal weather patterns or prey availability. Approximately half of the eagles were undetected using stopovers, but this could be caused by our sampling interval of one transmission/week. Eagles may have used stopovers ≤6 days and therefore were undetected. Distances traveled between stopover sites were similar on northbound and southbound migration, but low sample size may have reduced the power of the test.

Our results provide substantial information on Bald Eagle migratory timing, routes, and stopovers not described previously from banding and VHF telemetry studies. Detailed knowledge of eagle migration is important for managing this wide-ranging species. Eagles may benefit from a national or international management plan rather than current regional eagle plans. Conserving migratory stopover habitat should contribute to the continued health of the Bald Eagle population in Florida.

ACKNOWLEDGMENTS

We thank the following funding partners for making this research possible: Florida Nongame Wildlife Trust Fund; U.S. Fish and Wildlife Service, Atlanta, Georgia (Section 6 of the Endangered Species Act); USGS, Patuxent Wildlife Research Center; The University of Georgia, Warnell School of Forestry and Natural Resources; and Georgia Ornithological Society. T. F. Breen, Anthony Steffer, L. M. Phillips, N. J. Douglass, and S. K. Taylor contributed significantly to the initial phase of this study providing expertise in the field and office. G. W. Barrett, S. B. Castleberry, M. W. Collopy, Marco Restani, R. J. Warren, and two anonymous reviewers provided comments and suggestions that improved the manuscript. Movement, foraging and roosting locations, and stopover data are accessible on a web site (http://www.myfwc.com/eagle/) for managers to use in conserving Bald Eagle habitat in eastern North America.

LITERATURE CITED

Broley, C. L. 1947. Migration and nesting of Florida Bald Eagles. Wilson Bulletin 59:3–20.

Buehler, D. A., T. J. Mersmann, J. D. Fraser, and J. K. D. Seegar. 1991. Differences in distribution of breeding, non-breeding, and migrant Bald Eagles on the northern Chesapeake Bay. Condor 93:399–408.

ESRI. 1999. ArcView 3.2. Environmental Systems Research Institute, Redlands, California, USA.

Gerrard, J. M. and G. R. Bortolotti. 1988. The Bald Eagle: haunts and habits of a wilderness monarch. Smithsonian Institution Press, Washington, D.C., USA.

Gerrard, J. M., D. W. A. Whitfield, P. Gerrard, P. N. Gerrard, and W. J. Maher. 1978. Migratory movements and plumage of subadult Saskatchewan Bald Eagles. Canadian Field-Naturalist 92: 375–382.

Grubb, T. G., W. W. Bowerman, and P. H. Howey. 1994. Tracking local and seasonal movements of wintering Bald Eagles *Haliaeetus leucocephalus* from Arizona and Michigan with satellite telemetry. Pages 347–358 *in* Proceedings of the IV World Conference on Birds of Prey and Owls (B.-U. Meyburg and R. D. Chancellor, Editors). Pica Press, Berlin, Germany.

Harmata, A. R. 2002. Vernal migration of Bald Eagles from a southern Colorado wintering area. Journal of Raptor Research 36:256–264.

Harmata, A. R., J. E. Toepfer, and J. M. Gerrard. 1985. Fall migration of Bald Eagles produced in northern Saskatchewan. Blue Jay 43:232–237.

Heintzelman, D. S. 1975. Autumn hawk flights: the migrations in eastern North America. Rutgers University Press, Rutgers, New Jersey, USA.

Hunt, W. G., R. E. Jackman, J. M. Jenkins, C. G. Thelander, and R. N. Lehman. 1992. Northward post-fledging migration of California Bald Eagles. Journal of Raptor Research 26:19–23.

Laing, D. K., D. M. Bird, and T. E. Chubbs. 2005. First complete migration cycles for juvenile Bald Eagles (*Haliaeetus leucocephalus*) from Labrador. Journal of Raptor Research 39:11–18.

McClelland, B. R., L. S. Young, P. T. McClelland, J. G. Crenshaw, H. L. Allen, and D. S. Shea. 1994. Migration ecology of Bald Eagles from autumn concentrations in Glacier National Park, Montana. Wildlife Monographs 125.

Millsap, B., T. Breen, E. McConnell, T. Steffer, L. Phillips, N. Douglass, and S. Taylor. 2004. Comparative fecundity and survival of Bald Eagles fledged from suburban and rural natal areas in Florida. Journal of Wildlife Management 68: 1018–1031.

Natural Resources Canada. 2001. National topographic database: hydrography features. Centre for Topographic Information, Natural Resources Canada, Sherbrooke, Quebec, Canada.

Restani, M. 2000. Age-specific stopover behavior of migrant Bald Eagles. Wilson Bulletin 112:28–34.

SAS Institute Inc. 1999. SAS/STAT User's Guide. Version 8. SAS Institute Inc., Cary, North Carolina, USA.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry. W. H. Freeman and Company, New York, USA.

Steenhof, K., M. R. Fuller, M. N. Kochert, and K. K. Bates. 2005. Long-range movements and breeding dispersal of Prairie Falcons from southwest Idaho. Condor 107:481–496.

Sure!Maps Raster. 1995. Eastern U.S.: NH, VT, NY, MA, PA, RI, CT, NJ, DE, MD, DC, VA, WV, NC, SC, GA, FL, ME. Horizons Technologies Inc., San Diego, California, USA.

U.S. Geological Survey (USGS). 2003. U.S. National Atlas water feature areas: aqueducts, canals, dams, intercoastal waterways, rivers, and streams. Reston, Virginia, USA.

Weidensaul, S. 2000. The raptor almanac: a comprehensive guide to eagles, hawks, falcons, and vultures. Lyons Press, New York, USA.

Wood, P. B. and M. W. Collopy. 1994. Population ecology of sub-adult southern Bald Eagles in Florida: post-fledging ecology, migration patterns, habitat use, and survival. Final Report. Nongame Wildlife Program Project NG87-026. Florida Game and Fresh Water Fish Commission, Tallahassee, USA.

Wood, P. B., M. W. Collopy, and C. M. Sekerak. 1998. Postfledging nest dependence period for Bald Eagles in Florida. Journal of Wildlife Management 62:333–339.

The Wilson Journal of Ornithology 120(2):311–319, 2008

WETLAND FEATURES THAT INFLUENCE OCCUPANCY BY THE ENDANGERED HAWAIIAN DUCK

KIMBERLY J. UYEHARA,[1,4] ANDREW ENGILIS JR.,[2] AND BRUCE D. DUGGER[3]

ABSTRACT.—Habitat loss, introduced predators, and hybridization with feral Mallards (*Anas platyrhynchos*) continue to threaten the existence of the endangered Hawaiian Duck or Koloa maoli (*A. wyvilliana*). Protection and management of core breeding areas is a recovery objective, but lack of quantitative information on the species' habitat needs hinders recovery efforts. We conducted bi-monthly surveys of 48 wetlands on private lands on the Island of Hawai'i from March 2002 to June 2003. We compared Koloa use between seasons, wetland types, and study regions and modeled how use varied with 14 site and landscape variables. Koloa occupied 54% of the surveyed wetlands; use was higher on wetlands enhanced or created for Koloa primarily through the USDA's Wetlands Reserve Program (WRP) than on ponds created for agriculture (81 vs. 41%) and on wetlands in the Kohala than in the Mauna Kea region (93 vs. 38%). Koloa were more likely to use wetlands farther (>600 m) from houses, larger (>0.23 ha) wetlands, and those surrounded by more wetlands area (>1 ha). Our results (1) indicate WRP wetlands provide suitable habitat and (2) support wetlands enhancement or creation far from human disturbance. Habitat improvements combined with feral Mallard control may reduce extinction threats to Koloa. *Received 11 December 2006. Accepted 16 July 2007.*

The Hawaiian Duck or Koloa maoli (*Anas wyvilliana*), hereafter referred to as Koloa, is a monochromatic, non-migratory, endangered species allied with the North American Mallard (*A. platyrhynchos*) complex (Browne et al. 1993). With an approximate population of 2,200 birds (Engilis and Pratt 1993, Engilis et al. 2002), the Koloa is the only endemic duck species to remain in the main Hawaiian Islands of more than 11 members of Anatidae reported in the fossil record (Olson and James 1991, Burney et al. 2001). The breeding season is year-round with peaks in December to May on Kaua'i (Swedberg 1967) and April to June on Hawai'i (Giffin 1983). Koloa use diverse habitats from sea level to 3,000 m including palustrine emergent and riverine (Swedberg 1967, Giffin 1983, Engilis and Pratt 1993), but rarely estuarine (Engilis et al. 2002). Threats to Koloa persistence include depredation by introduced predators, habitat loss, and hybridization with feral Mallards (USDI 2005). Genetically-pure Koloa populations were believed to occur on the islands of Kaua'i (Browne et al. 1993, Rhymer 2001), Ni'ihau, and highlands of Hawai'i with hybrid swarms on O'ahu and Maui (Engilis and Pratt 1993), but there is now evidence of hybridization within pure populations (Engilis et al. 2002).

Habitat management of core breeding areas is a primary recovery objective for Koloa (USDI 2005). However, little is known about the basic ecology and habitat requirements of Koloa (Rhymer 2001, Engilis et al. 2002); thus, little specific information is available to guide habitat restoration. Wetlands were enhanced or created between 1999 and 2002 to improve habitat conditions on agricultural lands on the Island of Hawai'i through the USDA Natural Resources Conservation Service's Wetland Reserve Program (WRP) and other incentive programs (Ducks Unlimited's private lands initiative, North American Wetlands Conservation Act, and Partners for Fish and Wildlife). Wetland designs were based on limited field observations and earlier studies that indicated Koloa use should be higher in wetlands: (1) adjacent to other wetlands used by Koloa, (2) distant from human disturbance, (3) adjacent to streams, (4) containing an approximately 50:50 ratio of emergent plants to open water, (5) with an irregular shoreline, (6) free of introduced aquatic vertebrates, and (7) with controlled livestock grazing (Schwartz and Schwartz 1953; Swedberg 1967; Giffin 1983; K. A. Goebel, pers. comm.). These features are also considered important for North

[1] 73-1270 Awakea Street, Kailua-Kona, HI 96740, USA.

[2] Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, USA.

[3] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA.

[4] Corresponding author; e-mail: kjukem@lava.net

American dabbling ducks (Fredrickson and Dugger 1993, Weller 1999). No previous work has attempted to test the relative importance of these criteria on Koloa use or identify other criteria that might influence habitat suitability. This study was designed to: (1) characterize patterns of wetland use by Koloa, (2) compare characteristics of used and unused wetlands, and (3) examine how site and landscape characteristics influence wetland use by Koloa to guide future habitat enhancement projects.

METHODS

Study Area.—Our study was conducted in the Kohala-Mauna Kea region (20° 00′ N, 155° 25′ W) of Hawai'i, the largest and youngest island of the Hawaiian archipelago. The area studied was on the windward or northeast slopes of the Kohala and Mauna Kea mountains where the majority of mid-elevation depressional wetlands, agricultural ponds, and perennial streams occur because older volcanic substrates prevent percolation. A population of ~200 Koloa was re-established here by the State of Hawai'i captive propagation and release program (1958–80) after near extirpation of Koloa in the 1950s (Schwartz and Schwartz 1953, Giffin 1983, Engilis and Pratt 1993).

Field Methods.—We surveyed all known wetlands on two properties each in the Kohala and Mauna Kea regions consisting of 14 and 34 wetlands, respectively (n = 48) between 305 and 1,219 m in elevation (Fig. 1). The study sites included 16 WRP wetlands (6 in Kohala and 10 in Mauna Kea) and 32 agricultural ponds (8 in Kohala and 24 in Mauna Kea) which were stock ponds and small reservoirs constructed between 1900 and 2001. Wetland vegetation consisted primarily of *Schoenoplectus* spp. and *Myriophyllum aquaticum*. Upland vegetation consisted of livestock forage grasses (e.g., *Urochloa mutica*, *Pennisetum clandestinum*) and small patches or stands of trees (e.g., *Psidium* spp., *Metrosideros polymorpha*). Land uses included cattle ranching and macadamia nut, coffee, and koa (*Acacia koa*) farming.

We measured 14 characteristics for each wetland (42 sites characterized in Mar–Apr 2002; 6 in Sep 2002; Table 1). We used a Global Positioning System or digital U.S. Geological Survey topographic quadrangles to calculate wetland size, shoreline development (Lind 1974), distance to house, distance to stream, surrounding wetlands, stream length, and building density. We quantified emergent and aquatic plant cover using the point-intercept method (Higgins et al. 1996) with points taken on a 5 × 1 m, 5 × 5 m, or 10 × 10 m grid for wetlands <0.10, 0.10–0.30, or >0.30 ha, respectively. Data on the presence or absence of non-native waterfowl, fishes, bullfrogs (*Rana catesbeiana*), and livestock grazing were gathered during initial wetland characterization visits and subsequent bird surveys. We classified livestock grazing by the length of the grazing period: continuous (livestock were free ranging and had year-round access to wetlands), seasonal (wetlands were fenced and livestock had access during part of the year; e.g., non-breeding season), or no grazing.

We surveyed each wetland for Koloa at least twice per month from 1 March 2002 to 25 June 2003 (6 wetlands were added in Sep 2002), which included two peak nesting periods (Apr–Jun; Giffin 1983). Surveys were conducted during mornings (sunrise until 4 hrs after sunrise) and afternoons (4 hrs before sunset to sunset). We established 1–2 survey points at each wetland at spots that minimized disturbance and maximized visibility of water birds. We observed wetlands for 5–10 min with 10 × 42 binoculars and a 25–56 × spotting scope from each point. We recorded the number of Koloa present on each wetland for each survey. We recorded direction of movement to minimize duplicate counts if birds flew from an occupied wetland. We walked the wetland shoreline if no Koloa were observed from our survey points. We assumed all ducks matching morphological and behavioral descriptions in Engilis et al. (2002) were Koloa. Mallard × Koloa hybrid phenotypes have been recorded on the Island of Hawai'i (Engilis et al. 2002), but none was recorded at our study sites (1 Mallard male and 1 hybrid-like female observed in May 2003 in lowlands outside our survey area; KJU, pers. obs.). There were no field methods to distinguish Koloa from hybrids and few data on the prevalence of hybrids.

Statistical Analyses.—Birds on a wetland were unlikely to be undetected during a survey given the small size (0.01–1.3 ha) and

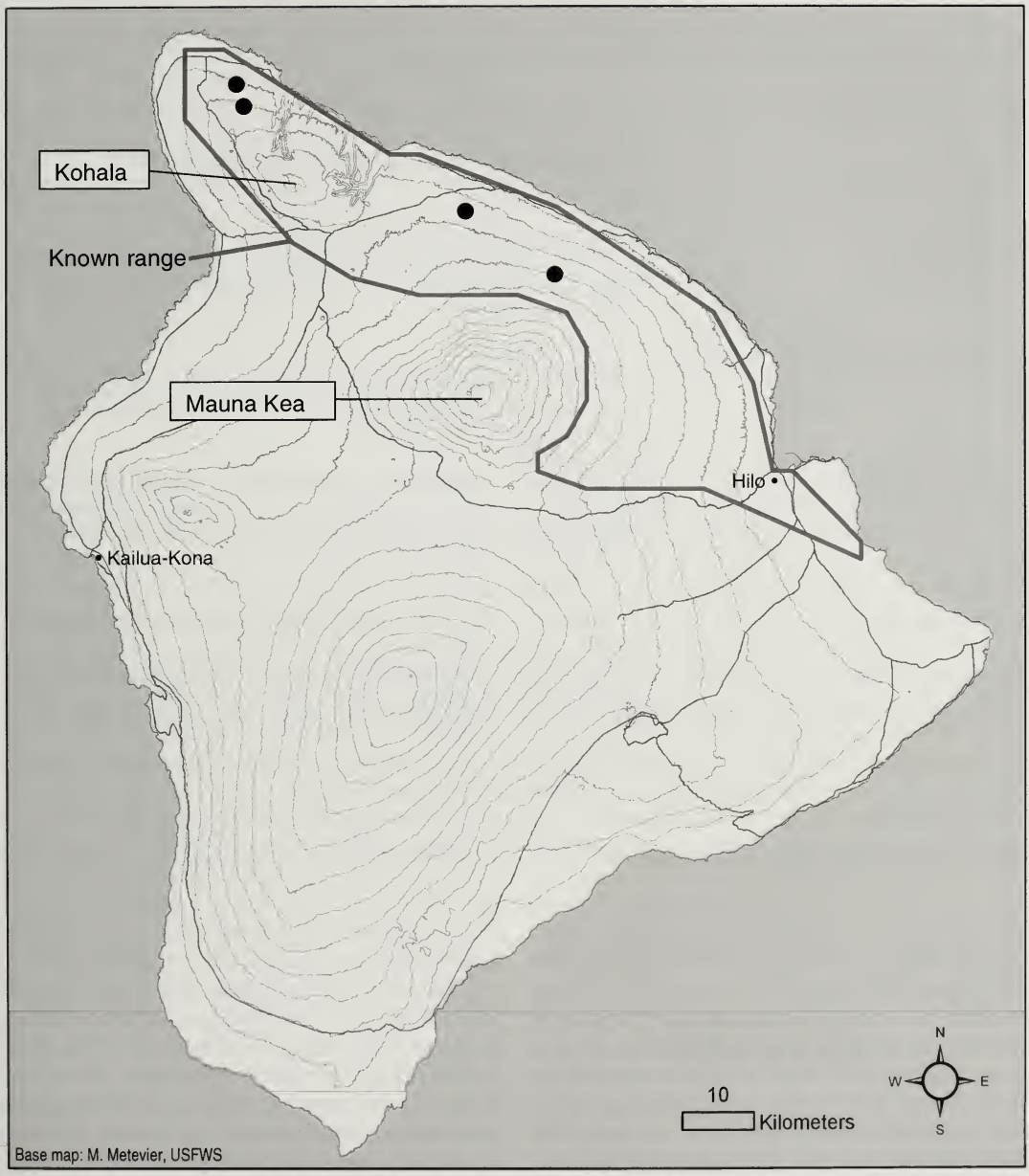


FIG. 1. Study sites (black dots) in the Kohala-Mauna Kea region of Hawai'i where wetlands were surveyed for presence of Koloa relative to the known range of Koloa on Hawai'i (gray line).

sparse vegetation of most wetlands, and we assumed a detection probability of 1.0. We assumed that birds were not concealed in vegetation or flushed without detection. A wetland was defined as "occupied" if Koloa were observed at least once during a survey. Multiple surveys (19–35 visits per wetland) were used to identify the status of a wetland and minimize assigning a wetland to the wrong category. Bias from undetected birds could result in conservative estimates of occupancy. However, we strived to identify wetlands with regular diurnal use and a wetland with an undetected bird would likely represent extremely low or nocturnal use, which was beyond the scope of our study. Data were untransformed.

TABLE 1. Site and landscape characteristics measured for 48 study wetlands surveyed for Koloa on the Island of Hawai'i during 2002.

Variable	Description
Site	
Wetland size	Estimated wetland area using GPS and GIS (ha)
Wetland vegetation structure (PCA of three variables)	
i. Open water	Percent area without vascular vegetation
ii. Emergent	Percent area with emergent vegetation (e.g., *Cyperus*, *Schoenoplectus*)
iii. Aquatic	Percent area with submergent or floating vegetation (e.g., *Myriophyllum*, *Nymphaea*)
Invasive species (presence of any one of the following)	
i. Non-native waterfowl	Ornamental or barnyard waterfowl in a domestic or semi-feral state (e.g., domestic Mallard breeds, such as Khaki Campbell, Pekin)
ii. Fishes	Cyprinids, poeciliids, or cichlids
iii. Bullfrogs	*Rana catesbeiana*
Grazing regime	Length of cattle or sheep grazing period (none, seasonal, continuous)
Shoreline development	Measurement of shoreline regularity; ratio of the shoreline length to the circumference of a circle with the same area as the wetland (1 = perfect circle)
Landscape	
Distance to house	Linear distance (m) from center of study wetland to nearest occupied house
Distance to stream	Linear distance (m) from center of study wetland to nearest intermittent or perennial stream
Surrounding wetlands	Percent wetland area within a 1-km radius from center of study wetland
Stream length	Intermittent or perennial stream km within a 1-km radius from center of study wetland (m/ha)
Building density	Number of houses and other structures within a 1-km radius from center of study wetland (*n*/ha)

We calculated occupancy rate as the proportion of wetlands occupied at least once by Koloa. We calculated percent occurrence as the number of surveys Koloa were present on a wetland divided by the total number of surveys. We assigned each survey to dry (May–Oct) or wet (Nov–Apr) and breeding (Jan–Jun) or nonbreeding (Jul–Dec) seasons. We used a likelihood ratio Chi-square test to compare occupancy rates and the Wilcoxon signed-rank test to compare percent occurrences between wetland categories (e.g., WRP vs. agricultural site).

We used logistic regression (Hosmer and Lemeshow 2000; SAS Institute 2001, 2005) in conjunction with an information-theoretic approach (Burnham and Anderson 2002) to examine habitat characteristics most closely associated with Koloa use. We examined bivariate relationships between explanatory variables using Spearman's rank correlation coefficient prior to modeling. Distance to house and building density ($r_s = -0.88$, $P < 0.0001$), distance to stream and stream length ($r_s = -0.74$, $P < 0.0001$), and surrounding wetlands and stream length ($r_s = 0.72$, $P < 0.0001$) were strongly correlated. Thus, we excluded one variable from each of the three pairs and retained distance to house, distance to stream, and surrounding wetlands. Measures of open water and emergent vegetation were correlated ($r_s = -0.82$, $P < 0.0001$); therefore, we used the first principal component (66% of total variance) from a PCA of these two variables and percent area with aquatic vegetation to represent vegetation structure in the wetland (eigenvectors = −0.71 for open water, 0.51 for emergent, and 0.48 for aquatic). We combined non-native waterfowl, fishes, and bullfrogs into one variable (invasive species) because introduced vertebrates may decrease habitat quality for

TABLE 2. Logistic regression identifying factors that influence occupancy of wetlands by Koloa on the Island of Hawai'i, 2002–2003, in order of increasing AIC_c value and decreasing Akaike weight (w_i). All models within 10 AIC values of the best model are presented.

Model	$-log(L)$[a]	K[b]	AIC_c	ΔAIC_c	w_i
Distance to house, Surrounding wetlands	21.787	3	50.119	0.00	0.338
Distance to house, Wetland size	22.248	3	51.041	0.92	0.213
Distance to house	23.627	2	51.521	1.40	0.168
Distance to house, Grazing regime	22.968	3	52.481	2.36	0.104
Distance to house, Invasive species	23.323	3	53.191	3.07	0.073
Distance to house, Distance to stream	23.591	3	53.182	3.61	0.056
Wetland size, Invasive species	23.970	3	54.485	4.37	0.038
Surrounding wetlands, Invasive species	26.120	3	58.785	8.67	0.004
Intercept only	33.104	1	68.295	18.18	0.000

[a] −log-likelihood.
[b] Number of variables.

waterfowl through competition for resources (Weller 1999).

Our selection of explanatory variables was *a priori*, but we could not reasonably develop a subset of multivariable models to compare. Thus, we examined all combinations of two-variable models (*a posteriori*) using variables from the first analysis that performed as well or better than the null model. We evaluated the relative strength of one- and two-variable models using ΔAIC_c and model weights (w_i), and the predictive ability of the best approximating models using concordance values. We considered models within 2.0 AIC values of the best model as competitive (Burnham and Anderson 2002). We evaluated parameter estimates within each model by investigating if confidence limits around the mean included zero and summing model weights for all models containing that variable (i.e., variable importance weight; Burnham and Anderson 2002). We used regression for variables associated with occupancy status to compare percent occurrence against the explanatory variable and *t*-tests to evaluate how slope estimates differed from zero, restricting our analysis to wetlands occupied by Koloa. Means ± SE and 95% confidence intervals are reported.

RESULTS

The wetlands had an occupancy rate of 54% and a mean percent occurrence of 9 ± 12% (range 0–46%) for Koloa. WRP wetlands had a higher occupancy rate (81%, $n = 16$) than agricultural ponds (41%, $n = 32$; $\chi^2 = 6.21$, df = 1, $P = 0.01$) and a higher percent occurrence (13 ± 3%) than agricultural ponds (7 ± 2%; $Z = 2.23$, $P < 0.03$). Wetlands at Kohala had both a higher occupancy rate (93 vs. 38%; $\chi^2 = 13.77$, df = 1, $P < 0.001$) and percent occurrence (20 ± 3% vs. 4 ± 1%; $Z = 4.13$, $P < 0.001$) than wetlands at Mauna Kea. Occupancy rates did not differ between wet versus dry season ($P = 1.00$) or breeding versus nonbreeding season ($P = 0.09$). However, Koloa had a tendency to occupy more wetlands during the breeding (46%, $n = 22$) than the nonbreeding (29%, $n = 14$) season. We combined data for all seasons when modeling the influence of habitat features on wetland use, and used all surveys of each wetland when calculating occupancy status.

Six variables performed as well or better than the null model including distance to house, wetland size, surrounding wetlands, grazing regime, invasive species, and distance to stream. The best approximating model, using these six variables in the multivariate analysis, was distance to house and surrounding wetlands ($w_i = 0.338$; $c = 84.4$) which received 1.6 times more support than the next best model (Table 2). Distance to house occurred in all six models and received the highest variable importance weight (0.952), followed in decreasing order by surrounding wetlands (0.344), wetland size (0.254), invasive species (0.115), grazing regime (0.105), and distance to stream (0.056). Only two models ranked above the single-variable model of distance to house, and the confidence intervals for parameter estimates included zero for all explanatory variables except distance to house.

Koloa used wetlands farther from houses (2,500 ± 261 m for occupied vs. 855 ± 209 m for unoccupied wetlands), larger wetlands (0.23 ± 0.06 ha for occupied vs. 0.06 ± 0.02 ha for unoccupied wetlands), and those surrounded by more wetland habitat (0.32 ± 0.04% occupied vs. 0.19 ± 0.03% for unoccupied). No wetland within 600 m of a house was used by Koloa suggesting human disturbance influenced use, but these wetlands (n = 12) also contained invasive species. All wetlands >600 m from houses that had invasive species (n = 8) were also used by Koloa. We discriminated between the influence of invasive species versus distance to house by controlling for distance to house, rerunning all six single-variable models using only wetlands >600 m from a house (n = 36). The only competitive model was wetland size (w_i = 0.952) and the confidence limits around the parameter estimate did not include zero. Percent occurrence for occupied wetlands (n = 26) was independent of surrounding wetlands (P = 0.23), increased with distance to house (t = 3.04, $P < 0.006$; Fig. 2), and was not linearly related to wetland size (P = 0.16). However, percent occurrence increased linearly with wetland size (t = 4.20, $P < 0.0004$; Fig. 2) when we restricted our analysis to wetlands <0.50 ha (n = 24) because the distribution of wetland size was inadequate to test for a relationship across the full range of sizes (only 2 of 26 wetlands were >0.50 ha and both were outliers being >10 SEs above the mean).

Wetland characteristics associated with Koloa use varied by wetland type and study region (Table 3). WRP wetlands were similar to agricultural ponds in size and the amount of surrounding wetlands, but averaged more than twice as far from houses. Wetlands at Kohala were on average almost three times farther from houses, larger, and in landscapes with more wetlands than those at Mauna Kea.

DISCUSSION

Koloa occupancy of WRP wetlands was high and our estimate of 81% is likely conservative since we also saw sign (feathers, tracks, droppings) at wetlands where birds were not observed. Koloa responded to new WRP wetlands within days of completion at Kohala and 3 months at Mauna Kea (KJU, pers. obs.). Higher Koloa use on WRP versus agricultural ponds indicates that WRP wetlands provided suitable Koloa habitat. Greater wetland remoteness and area contributed to higher Koloa use at Kohala than at Mauna Kea (Table 3). The low percent occurrence at study sites likely reflects the small Koloa population on Hawai'i. Population size may be constrained by a lack of sufficient wetlands habitat, but also may be a consequence of other limiting factors.

Koloa have been described as sensitive to disturbance (Swedberg 1967, Giffin 1983, Chang 1990, Engilis et al. 2002), consistent with our characterization. Koloa did not use any wetland within 600 m of a house. Distance to houses beyond 600 m did not influence wetlands occupancy; however, percent occurrence increased as distance increased. Distance to house was associated with other anthropogenic factors that may have discouraged use by Koloa. However, when we controlled for distance to house, wetland occupancy was not associated with invasive species or grazing regime suggesting human disturbance was most important. Koloa in other areas (e.g., river valleys on Kaua'i) may habituate to human activity. However, this is more common in landscapes characterized by larger wetland area intermixed with agriculture and dwellings (Engilis et al. 2002; KJU, pers. obs.). Our study wetlands were small (0.15 ± 0.04 ha, range 0.01–1.3 ha), kettle-shaped (shoreline development: 1.2 ± 0.02, range 1.0–1.7), and most were recently constructed or grazed and contained sparse emergent vegetation. This combination of features may make waterfowl more sensitive to disturbance than in larger wetlands, which generally provide greater escape cover that may buffer against human disturbance (Diefenbach and Owen 1989; KJU, pers. obs.) and have higher resource diversity (Brown and Dinsmore 1986, Weller 1999). Koloa occurred in wetlands as small as 141 m^2 indicating they will use small wetlands. However, both occupancy rate and percent occurrence increased with wetland size indicating larger wetlands up to 0.5 ha were used more consistently.

WRP sites were constructed near agricultural ponds already used by Koloa under the principle that a wetland complex is more attractive and productive than a similar but iso-

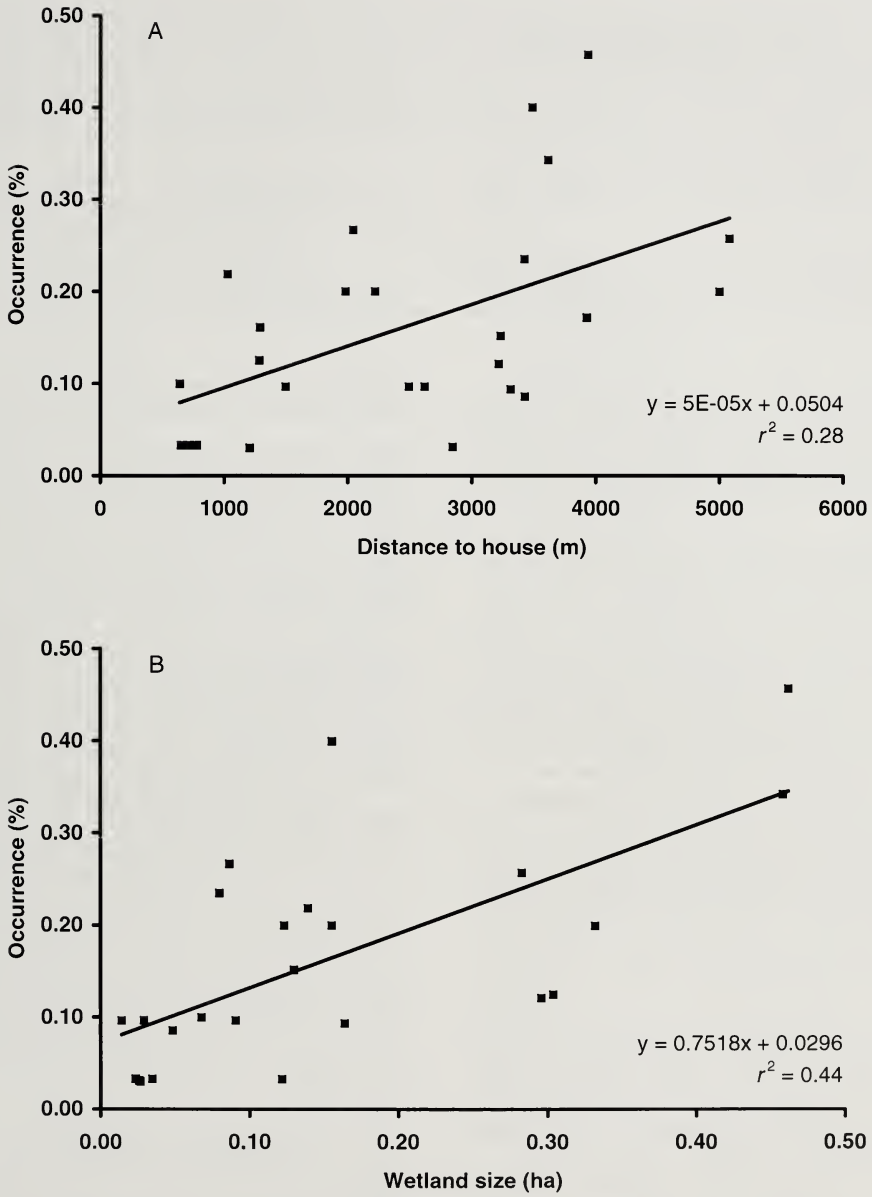


FIG. 2. Relationship between the percent occurrence of Koloa versus distance to house (A) and wetland size (B).

lated wetland (Forman 1995, Weller 1999). Koloa occupancy increased with wetland abundance supporting the concept of developing wetland complexes. This model received limited support, but Koloa did not abandon existing agricultural ponds following completion of WRP wetlands. Koloa were regularly observed moving among agricultural, stream, and new WRP habitats (KJU, pers. obs.).

Occupancy was not associated with shoreline development or vegetation structure as predicted because basin topography and vegetation communities of study sites were similar. Our measures for livestock grazing and invasive species were relatively crude, and a

TABLE 3. Wetland characteristics by wetland type (WRP vs. agricultural) and study area (Kohala vs. Mauna Kea) on the Island of Hawai'i, 2002–2003.

	Distance to house (m)	Surrounding wetlands (%)	Wetland size (ha)
Wetland type			
WRP (n = 16)	2,686 ± 309	0.23 ± 0.04	0.11 ± 0.02
Agricultural (n = 32)	1,276 ± 230	0.28 ± 0.03	0.18 ± 0.05
Study area			
Kohala (n = 14)	3,202 ± 1,317	0.48 ± 0.19	0.39 ± 0.36
Mauna Kea (n = 34)	1,147 ± 990	0.18 ± 0.09	0.05 ± 0.04

more focused study may reveal a stronger response by Koloa. Alternately, these variables may influence factors such as duckling survival instead of adult occupancy. We predicted juxtaposition of wetlands to streams may be important as, historically, high densities of Koloa were reported in streams (Schwartz and Schwartz 1953, Swedberg 1967, Giffin 1983). Koloa use did not vary by distance to stream, but our study sites were all within 1 km of a stream which was probably too small a scale to show variation in duck use. Thus, additional research is needed at a larger scale to evaluate if proximity to streams affects use.

Our models are descriptive, designed to provide baseline data about wetland characteristics that relate to Koloa use, and guide habitat restoration and management strategies for depressional wetlands on Hawai'i. Our findings indicate that managers should enhance or create wetlands >600 m from human dwellings, >0.23 ha in size, and in areas with >1 ha of surrounding wetland area within a 1-km radius. Beyond those minima, larger wetlands (up to 0.5 ha) and those farther from human disturbance received more frequent use (Fig. 2). These conditions, however, may be difficult to achieve in the relatively steep topography of mid-elevation Hawai'i; wetlands remote from human activity can present challenges for wetland managers.

Agricultural and small wetlands at Mauna Kea received less use by Koloa, but these wetlands may provide functional habitat, particularly when part of a wetland complex (Fredrickson and Dugger 1993, Semlitsch and Bodie 1998, Naugle et al. 2000, Engilis et al. 2002). Information on the daily and seasonal movements of Koloa is unknown, as is the optimal dispersion of wetlands. Tracking studies may be used to reveal use patterns and test detection probability assumptions. Studies that identify factors currently limiting Koloa population size are also needed; this information would allow for more effective conservation strategies and efficient use of conservation dollars. Private landowners, through WRP and other incentives, should be encouraged to enhance wetlands to increase habitat availability for Koloa. However, efforts to increase wetlands abundance will benefit not only Koloa, but feral Mallards and Mallard × Koloa hybrids, as evidenced by the rising population trends of Mallards and hybrids on some bird reserves on O'ahu and Maui, and recent sightings of hybrid phenotypes on Hawai'i (USDI 2005). Thus, it is essential that habitat improvements proceed in parallel with efforts to identify and remove Mallards and hybrids. Finally, occupancy is only one measure of habitat suitability. Information on how birds use wetlands would provide a better understanding of how wetlands are functioning to meeting life history needs of Koloa at Kohala and Mauna Kea.

ACKNOWLEDGMENTS

Financial and technical assistance was provided by Ducks Unlimited Inc., Delta Waterfowl Foundation, Bard College, USDA Natural Resources Conservation Service, USDI Fish and Wildlife Service, and the Hawai'i State Department of Land and Natural Resources. We are grateful to J. W. and M. T. Bailey, Bennett Dorrance Jr., Thuy Fujimoto, M. S. Gomes, E. L. and H. T. Gunther, and D. M. Matsuura for providing access to their land and logistical support. We thank K. M. Dugger, T. A. Erickson, K. A. Goebel, J. M. Higashino, Erik Kiviat, A. P. Marshall, and K. E. Moore for technical support and review of drafts of the manuscript. This publication was improved by the comments of M. H. Reynolds and an anonymous peer reviewer.

LITERATURE CITED

Brown, M. and J. J. Dinsmore. 1986. Implications of marsh size and isolation for marsh bird management. Journal of Wildlife Management 50:392–397.

Browne, R. A., C. R. Griffin, P. R. Chang, M. Hubley, and A. E. Martin. 1993. Genetic divergence among populations of the Hawaiian Duck, Laysan Duck, and Mallard. Auk 110:49–56.

Burney, D. A., H. F. James, L. P. Burney, S. L. Olson, W. Kikuchi, W. L. Wagner, M. Burney, D. McCloskey, D. Kikuchi, F. V. Grady, R. Gage II, and R. Nishek. 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. Ecological Monographs 71: 615–641.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, USA.

Chang, P. R. 1990. Strategies for managing endangered waterbirds on Hawaiian National Wildlife Refuges. Thesis. University of Massachusetts, Amherst, USA.

Diefenbach, D. R. and R. B. Owen Jr. 1989. A model of habitat use by breeding American Black Ducks. Journal of Wildlife Management 53:383–389.

Engilis Jr., A. and T. K. Pratt. 1993. Status and population trends of Hawaii's native waterbirds, 1977–1987. Wilson Bulletin 105:142–158.

Engilis Jr., A., K. J. Uyehara, and J. G. Giffin. 2002. Hawaiian Duck (*Anas wyvilliana*). The birds of North America. Number 694.

Forman, R. T. T. 1995. Some general principles of landscape and regional ecology. Landscape Ecology 10:133–142.

Fredrickson, L. H. and B. D. Dugger. 1993. Management of wetlands at high altitudes in the Southwest. Technical Report. USDA, Forest Service, Albuquerque, New Mexico, USA.

Giffin, J. G. 1983. (1) Abundance and distribution of Koloa on the Island of Hawaii. (2) Movements, survival, reproductive success and habitat of Koloa on the Island of Hawaii. Pittman-Robertson Projects W-18-R-7 and W-18-R-8, Job R-III-H. Technical Report. Hawaii Division of Fish and Game, Honolulu, USA.

Higgins, K. F., J. L. Oldemeyer, K. J. Jenkins, G. K. Clambey, and R. F. Harlow. 1996. Vegetation sampling and measurement. Pages 567–591 *in* Research and management techniques for wildlife and habitats (T. A. Bookhout, Editor). Fifth Edition. The Wildlife Society, Bethesda, Maryland, USA.

Hosmer, D. W. and S. Lemeshow. 2000. Applied logistic regression. Second Edition. John Wiley and Sons, New York, USA.

Lind, O. T. 1974. Handbook of common methods in limnology. C. V. Mosby Company, St. Louis, Missouri, USA.

Naugle, D. E., K. F. Higgins, M. E. Estey, R. R. Johnson, and S. M. Nusser. 2000. Local and landscape-level factors influencing Black Tern habitat suitability. Journal of Wildlife Management 64:253–260.

Olson, S. L. and H. F. James. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands. Part I. Non-Passeriformes. Ornithological Monographs 45:1–88.

Rhymer, J. M. 2001. Evolutionary relationships and conservation of the Hawaiian anatids. Studies in Avian Biology 22:61–67.

SAS Institute Inc. 2001. SAS®. Version 8.2. SAS Institute, Cary, North Carolina, USA.

SAS Institute Inc. 2005. JMP-IN®. Version 5. SAS Institute, Cary, North Carolina, USA.

Schwartz, C. W. and E. R. Schwartz. 1953. Notes on the Hawaiian Duck. Wilson Bulletin 65:19–25.

Semlitsch, R. D. and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129–1133.

Swedberg, G. E. 1967. The Koloa. Technical Report. Hawaii Division of Fish and Game, Honolulu, USA.

U.S. Department of the Interior (USDI). 2005. Draft revised recovery plan for the Hawaiian waterbirds. Second Revision. USDI, Fish and Wildlife Service, Portland, Oregon, USA.

Weller, M. W. 1999. Wetland birds: habitat resources and conservation implications. Cambridge University Press, New York, USA.

The Wilson Journal of Ornithology 120(2):320–330, 2008

HABITAT FEATURES ASSOCIATED WITH BARROW'S GOLDENEYE BREEDING IN EASTERN CANADA

MICHEL ROBERT,[1,3] BRUNO DROLET,[1] AND JEAN-PIERRE L. SAVARD[2]

ABSTRACT.—We investigated environmental variables linked to presence of Barrow's Goldeneye (*Bucephala islandica*) pairs from the eastern North American population on 412 lakes of the Sainte-Marguerite River watershed, Québec, Canada. We analysed habitat relationships at two spatial scales (i.e., considering all lakes surveyed and high elevation lakes only) and predetermined the high elevation lakes as those including 90% of Barrow's Goldeneye occurrences. Barrow's Goldeneye were found on 59 lakes, all of which were ≥490 m elevation (maximum = 822 m) with 90% at ≥610 m. Six variables tested using multivariate logistic regressions contributed to explain the occurrence of goldeneyes. Four were significant ($P < 0.10$) in both the complete and the high elevation data sets: nest boxes (+) and brook trout (*Salvelinus fontinalis*) (−) occurrences, altitude (+), and the interaction between altitude and mean slope (+). The models explained only a small proportion of Barrow's Goldeneye occurrence for both data sets ($R^2 = 0.27$ and 0.23, respectively). The negative relationship between Barrow's Goldeneye and brook trout occurrences, and the positive relationship with altitude probably reflect a positive relationship between goldeneye and highly productive aquatic ecosystems. Barrow's Goldeneye from eastern North America primarily use high altitudinal, productive lakes during the breeding season, which emphasizes the importance of fishless lakes for that population at risk. *Received 16 January 2007. Accepted 7 September 2007.*

Barrow's Goldeneye (*Bucephala islandica*) has a discontinuous distribution; it occurs mostly in western North America (~180,000 individuals) with smaller populations in eastern North America (~6,000) and Iceland (~2,000) (Eadie et al. 2000, Einarsson et al. 2006, Robert and Savard 2006). Birds from the western North American population during the breeding season are predominantly associated with alkaline lakes in parkland areas, but also with alpine and sub-alpine lakes, American beaver (*Castor canadensis*) ponds, and small sloughs (Eadie et al. 2000). No landscape-scale study has investigated habitat attributes associated with these breeding sites, but evidence suggests they are usually highly productive and invertebrate-rich (Savard et al. 1994, Evans 2003). Similarly, birds from the Icelandic population are largely confined to the invertebrate-rich areas of Lake Mývatn and Laxá River (Einarsson 1990, Gardarsson and Einarsson 2004).

Birds from the eastern North American population were thought to breed above tree-line in northeastern Canada (Palmer 1976, AOU 1998), but recent studies have shown their core breeding area to be much further south in large tracts of boreal forest north of the St. Lawrence River Estuary and Gulf in southeastern Canada (Robert et al. 2000b, 2002). The birds reported by Robert et al. (2000b) were mainly on small (<10 ha), high elevation (>500 m), headwater lakes in forests dominated by black spruce (*Picea mariana*) and feather moss, or by balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*). Nothing is known about the specific habitat requirements of this small population, which may comprise <2,000 pairs (Robert and Savard 2006) and is on the List of Wildlife Species at Risk of Canada under the *Species at Risk Act* (Government of Canada 2007).

We conducted helicopter surveys of goldeneye pairs in the core breeding area of the eastern North American population of Barrow's Goldeneye with the specific objectives to identify: (1) habitat features, and (2) environmental variables associated with this population. These data will be used to contribute in the production of a management plan identifying conservation needs for this population at risk and its habitats.

METHODS

Study Area.—The area studied was in the Sainte-Marguerite River drainage basin (1,600 km²), Québec, Canada on the north shore of

[1] Canadian Wildlife Service, Environment Canada, 1141 Route de l'Église, P. O. Box 10100, Québec, QC, G1V 4H5, Canada.

[2] Science and Technology, Environment Canada, 1141 Route de l'Église, P. O. Box 10100, Québec, QC, G1V 4H5, Canada.

[3] Corresponding author;
e-mail: michel.robert@ec.gc.ca

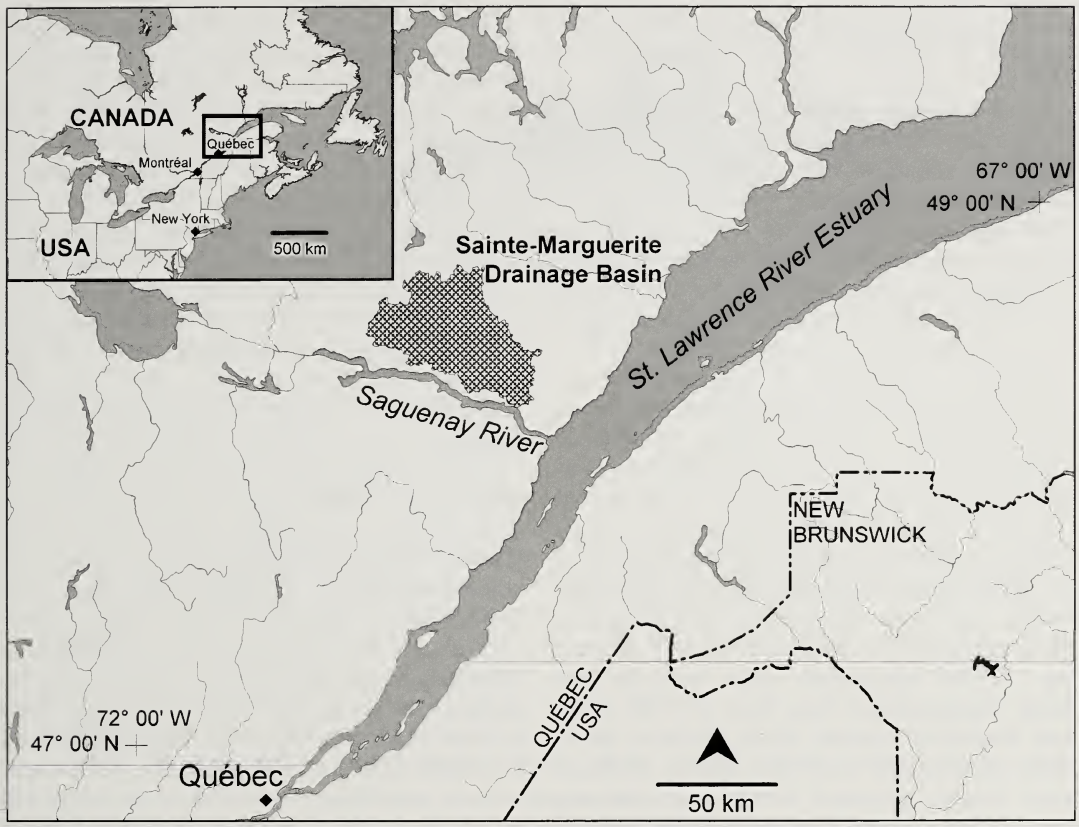


FIG. 1. Sainte-Marguerite River watershed in the balsam fir-white birch bioclimatic domain of the boreal forest in Québec, Canada.

the St. Lawrence River Estuary north of the Saguenay River (Fig. 1). It comprises 968 lakes with a mean (± SD) surface area of 13.2 ± 5.3 ha. The area is rugged with mountains (mean altitude = 607 ± 187 m) intersected by steep river valleys. The climate is cold, wet, and strongly seasonal. Mean annual temperature is 0° C with annual precipitation between 100 and 130 cm. Annual snowfall is between 350 and 400 cm. The area is in the balsam fir-white birch bioclimatic domain (Wiken 1986, Robitaille and Saucier 1998) of the Laurentian Highlands physiographic region (Desponts 1996), and is primarily used for commercial timber production and recreational fishing. Goldeneye nest boxes were installed around 62 of the lakes of the study area in fall 1998 and 1999 (Savard and Robert 2007).

Lake Sampling and Goldeneye Surveys.— We randomly selected 412 lakes in the Sainte-Marguerite River watershed based on surface area and elevation (Robert et al. 2000b): 58% were lakes 1–10 ha and >300 m, 22% were 10–100 ha and >300 m, 10% were 1–100 ha and 0–300 m, and 10% were 0.2–1.0 ha at all elevations. Lakes were surveyed once by helicopter (Bell 206 L equipped with bubble-type rear windows) between 28 May and 1 June 2001 noting the presence of Barrow's and Common (*Bucephala clangula*) goldeneyes; a lone male or a pair of each species was considered as a pair occurrence for a given lake. Flights over lake margins were at an altitude 10–50 m and flight speed varied from 50 to 100 km/hr, depending on the complexity of aquatic habitats, atmospheric conditions, and topography. Goldeneyes were identified by two observers, a navigator in front of the helicopter and a compiler at the rear of the cabin on the same side as the navigator. The same observers were used in all surveys. Barrow's Goldeneye were distinguished from Common Goldeneye from the air by their distinctive, darker upperwing pattern and, when

possible, by the males' facial crescent or the females' bill color (Tobish 1986, Eadie et al. 2000).

Environmental Variables.—Considering our sample size and remote study area, most environmental variables were derived from satellite imagery and topographic maps. This underscores the exploratory nature of the study and lack of *a priori* models. We investigated the relationships between goldeneye occurrence and 20 environmental variables, including the presence of nest boxes at some lakes ($n = 32$), which were considered as a covariable. Fish occurrence was estimated using data for brook trout (*Salvelinus fontinalis*) from the Québec Ministère des Ressources naturelles et de la Faune (Jean Tanguay, pers. comm.). Lakes without trout were considered as fishless, as this is typically the only fish species inhabiting lakes of the study area (Lacasse and Magnan 1994). The surface area (ha), altitude (m), and number of lakes upstream were measured for each lake using 1:50,000 topographic maps from the National Topographical Data Base (NTDB) (Natural Resources Canada 2005). Relative abundance of emergent rocks and riparian wetlands were visually estimated during helicopter surveys, using a semi-quantitative scale ranging from one (little or none) to three (many). Mean slope (%) was measured in a 500-m zone radiating from the lake's perimeter using maps from the NTDB and the pixel interpolation method based on a 25-m^2 pixel grid and a 7×7 pixel calculation window using a smoothed diagonal search (module GRDINT) (Carrara 1988, PCI 2001). All other variables were obtained from a Landsat TM5 multispectral satellite image of the study area taken on 4 June 1999 (VIASAT 2001), which contained radiometric information in seven spectrally defined channels. Habitats were mapped using a supervised classification approach with classes defined *a priori.* The spectral signature (radiance) of a given habitat class was assigned by sampling pixels known to belong to a given class. Habitat classes were validated using Québec Ministère des Ressources naturelles et de la Faune 1:20,000 forest maps dating from 1999 and field data collected on 20–21 September 2001 ($n = 35$ plots). We used the software ENVI (2005) to evaluate differences between spectral signatures of habitat classes. A first filter was used to exclude all clear-cut areas and reduce confusion between mixed forest and regeneration stands. A second filter was used to exclude all burned areas to reduce confusion between recent burns and recent clear-cuts. Each pixel was assigned to one of 15 different habitat classes using a maximum likelihood approach with a minimum probability level of 80% resemblance. Eight homogeneous patch types were developed after classification: open water (deep water and shallow water combined), wetlands (marshes, exploited and natural peatlands), exposed mineral (mainly logging roads), recent clear-cuts (0–5 years or filter 1 and 5–10 years post clear-cuts combined), recent burns (filter 2), regeneration (10–20 years post clear-cuts and deciduous regeneration combined), mature deciduous and mixed forests combined, and mature conifer forests (dense and scarce conifer stands combined). The classified image was smoothed using a 3×3 filter (Majority 3×3) (ENVI 2005). The raster version of the classified image was analysed using FRAGSTAT (McGarigal and Marks 1995). We calculated the surface area of all patch types for each lake in a 2-km zone radiating from its perimeter and converted these surfaces areas into percentages without considering the portion of the image obscured by cloud cover (mean $\pm$ SD = 0.09 $\pm$ 0.4%). We measured four lake configuration indices in a 16-km^2 (4×4 km) plot centered on each surveyed lake: number of lakes, mean surface area of lakes (ha), lakes mean nearest-neighbor distance (m), and lake mean shape index (1 for round lakes and >1 for irregularly shaped lakes).

Habitat Relationships.—We verified the linearity of relationships between the presence of Barrow's Goldeneye pairs and environmental variables individually using a graph of the $\text{logit}(p) = \log(p/[1 - p])$ according to five balanced classes of the explanatory variable, where p is the frequency of Barrow's Goldeneye for each of the five classes. Ten variables had non-linear relationships with goldeneye occurrence. Lake surface area, mean slope, and coniferous forests had quadratic relationships and were transformed. The other variables (number of lakes upstream [<2 lakes or more], riparian wetlands [class 1 or class 2 and 3], wetlands [≤0.7% or greater], exposed mineral [≤0.2% or greater], recent burns [<2% or greater], regeneration [<7% or greater], and number of lakes [<18 lakes or

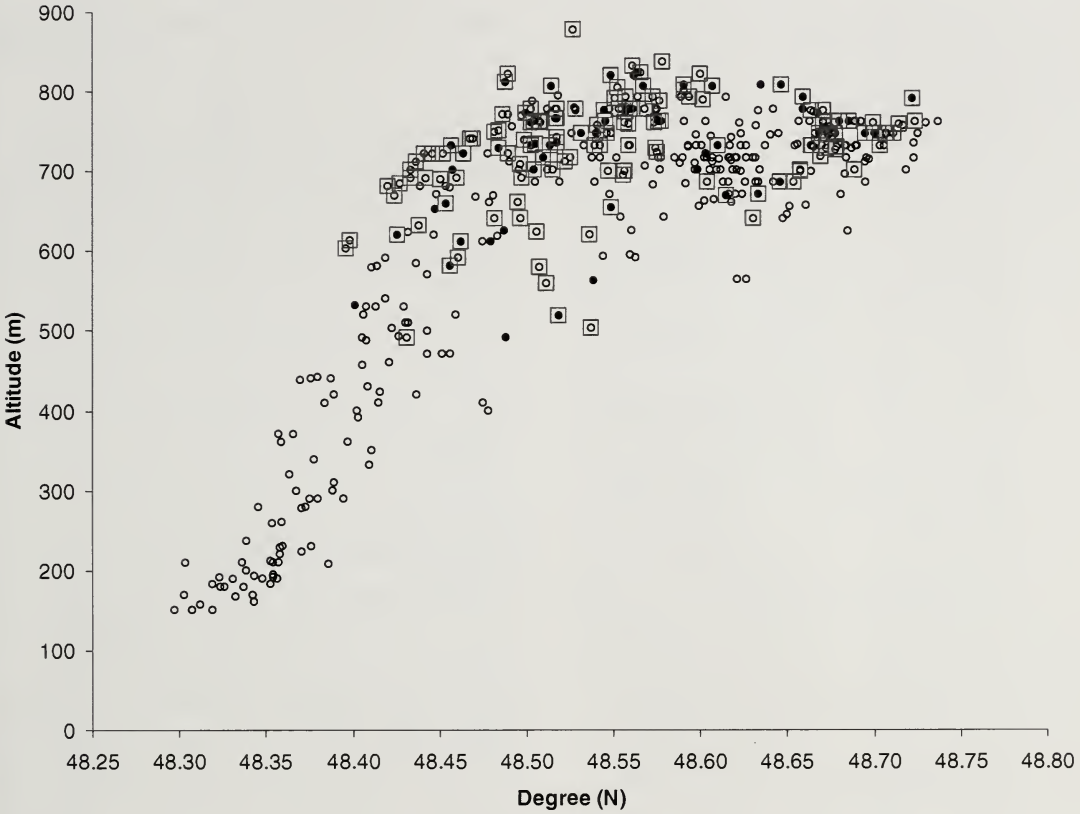


FIG. 2. Distribution by latitude and altitude of 412 lakes surveyed in the Sainte-Marguerite River drainage basin, Québec, Canada. Black and white dots denote lakes with (observed occurrences) or without (observed absences) Barrow's Goldeneye, respectively. Gray squares identified lakes that were predicted as occupied by Barrow's Goldeneye according to a logistic probability level obtained from a ROC analysis.

greater]) were transformed as categorical variables in a binary format.

We used univariate and multivariate (stepwise selection) logistic regressions to assess relationships between the occurrence of Barrow's Goldeneye pairs and environmental variables (Proc Logistic) (SAS Institute Inc. 2001). Highly redundant variables (variance inflation >20) and variables with a probability level >0.25 calculated from univariate analyses were excluded from the multivariate analysis. Because of the large sample size (n = 412) and to minimize the risk of spurious significant correlations, significance levels were set at 0.15 and 0.10 to include or keep, respectively, a variable in multivariate analysis. The maximum rescaled coefficient of determination (r^2) (Nagelkerke 1991) was calculated to evaluate the contribution of each variable to the multivariate analysis.

We analyzed habitat relationships at two spatial scales considering all lakes surveyed and high elevation lakes only. We predetermined high elevation lakes as those including 90% of Barrow's Goldeneye occurrences. Models resulting from both data sets were assessed using the same data for training and testing (resubstitution). We used the crossover of misclassification rates (sensibility vs. [1 − specificity]) in a receiver-operating characteristic (ROC) analysis to examine the optimum probability threshold at which Barrow's Goldeneye should occur (Cody and Smith 1997). A confusion matrix was built using this threshold to evaluate sensitivity (proportion of true presence predicted), overall prediction success (proportion of true presence and absence predicted), and Kappa, a measure of the proportion of all possible cases of presence or absence that are predicted correctly after ac-

TABLE 1. Relationships derived from univariate logistic regressions between spring occurrence of Barrow's Goldeneye pairs on lakes of the Sainte-Marguerite River drainage basin, Québec, Canada, and associated environmental variables. Values are presented for all lakes surveyed (n = 412) and for lakes ≥610 m (i.e., lakes with 90% of Barrow's Goldeneye occurrences) with (n = 54) or without (n = 252) Barrow's Goldeneye. Superscripts indicate if variables were measured either at the lake level (a), in the watershed area (b), in a 500-m (c) or a 2-km (d) zones radiating from the lake's perimeter, or in a 16 km² plot centered on the surveyed lake (e).

	All lakes (n = 412)							Lakes ≥610 m (n = 306)									
								With Barrow's Goldeneye				Without Barrow's Goldeneye						
	Min	Max	Mean	CV	P	r^2	C	Min	Max	Mean	CV	Min	Max	Mean	CV	P	r^2	C
Nest box occurrence[a]	380	32	n/a	n/a	<0.001	0.06	+	42	12	n/a	n/a	233	19	n/a	n/a	<0.01	0.05	+
Fish occurrence[a]	133	279	n/a	n/a	<0.001	0.08	−	30	24	n/a	n/a	71	181	n/a	n/a	<0.01	0.08	−
Lake surface area (ha)[a]	0.3	88	9	155	0.13			0.5	20	7	62	0.3	88	10	156	0.14		
Lake altitude (m)[a]	150	877	635	28	<0.001	0.10	+	610	822	739	8	610	877	724	6	0.03	0.03	+
Lakes upstream (n)[b]	0	15	1.4	170	<0.01	0.05	−	0	4	0.6	142	0	14	1.5	156	0.01	0.06	−
Emergent rocks (3 classes)[a]	1	3	1.5	45	<0.01	0.04	+	1	3	1.8	45	1	3	1.6	43	0.04	0.02	+
Riparian wetlands (3 classes)[a]	1	3	1.5	51	0.02	0.02	−	1	3	1.3	49	1	3	1.5	50	0.02	0.03	−
Mean slope (%)[c]	2	32	14	40	0.43			5	26	15	32	2	27	12	40	<0.01	0.05	+
Open water (% area)[d]	0.1	19	7	59	0.85			0.9	16	7	57	0.4	19	7	50	0.35		
Wetlands (% area)[d]	0.01	5	0.7	104	<0.01	0.06	−	0.01	2	0.5	108	0.01	4	0.7	109	0.04	0.02	−
Exposed mineral (% area)[d]	0	9	1.9	95	0.14			0	5	1.5	94	0	7.9	2.1	88	0.68		
Recent clear-cuts (% area)[d]	0	65	12	122	0.22			0.01	56	15	83	0	65	16	104	0.93		
Recent burns (% area)[d]	0	35	0.7	547	0.62			0	1	0.05	396	0	34	1	435	0.17		
Regeneration (% area)[d]	0.1	59	15	100	<0.01	0.07	+	0.1	59	22	71	0.07	55	18	79	0.07	0.02	+
Mature deciduous/mixed forests (% area)[d]	0.6	95	34	93	0.10			1	82	23	104	0.6	93	18	106	0.11		
Mature conifer forests (% area)[d]	0.8	86	29	74	0.81			2	86	31	69	4	86	37	57	0.13		
Number of lakes[e]	4	38	21	35	0.33			6	36	20	35	6	38	23	31	0.02	0.03	−
Lakes mean surface area (ha)[e]	0.4	17	4	56	0.59			1.5	11	5	49	0.6	17	5	50	0.72		
Lakes mean nearest-neighbor distance (m)[e]	67	747	208	43	<0.01	0.03	+	124	531	230	37	67	747	202	39	0.02	0.03	+
Lake mean shape index[e]	1.2	2.5	1.5	9	0.67			1.3	1.8	1.5	7	1.2	2.0	1.5	7	0.84		

counting for chance effects (Fielding and Bell 1997).

RESULTS

Barrow's Goldeneye were found on 59 (14.3%) lakes, Common Goldeneye on 32 (7.8%), and both species on 6 (1.5%); 79.4% (n = 327) of the lakes surveyed had no goldeneye. Only one lake had more than one (i.e., 2) Barrow's Goldeneye pair. All Barrow's Goldeneye were on lakes ≥490 m (maximum = 822 m) elevation and 90% were at an altitude ≥610 m (i.e., the threshold we used to create the high elevation data set [n = 306, 17.6% of lakes with Barrow's Goldeneye]) (Fig. 2). Common Goldeneye were found at a broader range of altitudes (190–822 m) and 31% were on lakes <610 m. We chose not to analyze Common Goldeneye data considering low occurrence of the species and the lake sampling design, which tended to favor Barrow's Goldeneye.

Univariate Logistic Regressions.—Barrow's Goldeneye occurrence was higher ($P < 0.10$) on lakes with nest boxes, no fish, none or few lakes upstream, many emergent rocks, none or few riparian wetlands, and at high elevation in landscapes with low proportion of wetlands, high proportion of regeneration, and high mean nearest-neighbor distances. The same environmental variables were selected ($P < 0.10$) when considering only the high elevation data set. The occurrence of Barrow's Goldeneye was also higher ($P < 0.10$) on high elevation lakes with high mean slopes and in landscapes with low number of lakes (Table 1).

Multivariate Logistic Regressions.—Six variables tested explained the occurrence of Barrow's Goldeneye (Table 2). Four were significant ($P < 0.05$) in both the complete and the high elevation data sets: nest boxes (+), fish occurrence (−), altitude (+), and the interaction between altitude and mean slope (+). The number of lakes upstream (−) was significant (P = 0.07) only in the complete data set, and riparian wetlands (−) only in the high elevation data set (P = 0.03). Most relationships were highly significant ($P \leq 0.01$), but models explained only a small proportion of Barrow's Goldeneye occurrence for both the complete and high elevation data sets (R^2 = 0.27 and R^2 = 0.23, respectively) (Table 2).

The cross-over of misclassification rates in-

TABLE 2. Models derived from multivariate logistic regressions (stepwise selection; α = 0.1) between spring occurrence of Barrow's Goldeneye pairs on lakes of the Sainte-Marguerite River drainage basin, Québec, Canada, and associated environmental variables. Two models are presented: one for all lakes surveyed (n = 412; goldeneye occurrence = 14%) and one for lakes ≥610 m, i.e., lakes including 90% of all goldeneye occurrences (n = 306; goldeneye occurrence = 18%). Superscripts indicate if variables were measured at the lake level (a) or in the watershed area (b). The presence of nest boxes was considered as a covariable. Variables with a probability level >0.25 as calculated from univariate analyses (Table 1) were excluded from the analysis.

	All lakes (n = 412)					Lakes ≥610 m (n = 306)				
	χ^2	b	90% CI	P	R^2_p	χ^2	b	90% CI	P	R^2_p
Nest box occurrence[a]	14.8	0.67	1.05 to 0.29	<0.01	0.06	8.7	0.63	1.02 to 0.23	<0.01	0.05
Fish occurrence[a]	25.8	−0.55	−0.28 to −0.83	<0.01	0.10	19.8	−0.54	−0.25 to −0.83	<0.01	0.10
Lake altitude[a]	12.1	0.007	0.004 to 0.01	<0.01	0.06	8.3	0.01	0.01 to 0.02	<0.01	0.02
Mean slope[a] X Lake altitude[a]	7.5	1.5 E-05	5.67 E-06 to 2.4 E-05	0.01	0.03	4.0	2.0 E-05	9.4 E-06 to 3.03 E-05	0.05	0.02
Number of lakes upstream[b]	3.3	−0.65	−0.11 to −1.39	0.07	0.02					
Riparian wetlands[a]						4.5	−0.38	−0.06 to −0.72	0.03	0.04
Intercept		−7.34	−10.39 to −4.81	<0.01			−10.44	−15.82 to −5.36	<0.01	

dicated that lakes with a logistic probability level >0.173 could be predicted to be occupied by Barrow's Goldeneye. The confusion between predicted and observed occurrences indicated, for both the complete and high elevation data sets, a low sensitivity (31 and 32%, respectively) and Kappa (30 and 25%, respectively) values, but a high overall prediction success (72 and 71%, respectively) because of the high prevalence of absences well predicted (Fig. 2).

DISCUSSION

This study is the first to explore habitat relationships for Barrow's Goldeneye breeding in eastern North America. The multivariate models explained only a small portion of the variance, but there was a strong and significant link between some variables and the occurrence of Barrow's Goldeneye for both the complete data set and high elevation lakes. We found a clear negative relationship with brook trout occurrence. Abundance, diversity, and assemblage characteristics of aquatic insects vary with respect to fish populations as fish predation may, for example, eliminate or reduce the abundance of nekton or cause them to mature at smaller size (Pope et al. 1973, Pope and Carter 1975, Bendell and McNicol 1987, Chess et al. 1993). Mallory et al. (1994) found that fish status of a lake was a reliable cue to invertebrate abundance in boreal wetlands. Goldeneyes rely on aquatic invertebrates for food (Bendell and McNicol 1995, Eadie et al. 2000) and food competition by fish may affect their use of habitat (Eriksson 1979, Eadie and Keast 1982, DesGranges and Gagnon 1994, Pöysä et al. 1994). We believe the negative relationship between Barrow's Goldeneye and brook trout occurrences reflects a positive relationship between goldeneye and highly productive aquatic ecosystems. Barrow's Goldeneye from other populations, worldwide, have also been linked to productive habitats, as they occur on small, shallow, alkaline fishless lakes in the Cariboo Parklands of central British Columbia (Topping and Scudder 1977, Boyd and Savard 1987, Boyd and Smith 1989, Evans 2003) and invertebrate-rich volcanic areas of Lake Mývatn and upper Laxá River in Iceland (Einarsson 1988, 1990; Gardarsson and Einarsson 2004). The drainage basin where we conducted our study historically had at least 185 fishless lakes >2 ha (Jean Tanguay, Ministère des Ressources naturelles et de la Faune du Québec, unpubl. data), and is an important area of the Laurentian Highlands for brook trout allopatry and fishless lakes. Its high altitude and rugged topography precluded many lakes from being recolonized by brook trout after the Wisconsin glaciation (Pope et al. 1989, Lacasse and Magnan 1994).

Barrow's Goldeneye occurrence was clearly associated with altitude, as the species was absent below 490 m. Barrow's Goldeneye reported by Robert et al. (2000b) were also on high elevation lakes, 54% of them above 500 m. It is difficult to dissociate elevation from fishless lakes, as a large proportion occurs at the head of watersheds at high elevation in our study area. The information we obtained on occurrence of brook trout may have been imperfect, because illegal stocking of fishless lakes is known to occur in our study area (Jean Tanguay, pers. comm.). This may have enhanced the relative importance of altitude, because lakes at higher altitudes are less readily accessible for fish stocking than those at lower elevation. The relationship between goldeneyes and altitude may also be related to competition, considering the larger, more aggressive Barrow's Goldeneye may dominate the smaller Common Goldeneye (Savard 1984, Savard and Smith 1987), which is also known to favor lakes without fish (Eriksson 1979, Eadie and Keast 1982, Pöysä and Virtanen 1994). Common Goldeneye were numerous in the valley below our study area and Barrow's Goldeneye did not occur there (Sénéchal 2003) supporting the association of Barrow's Goldeneye with high elevation lakes. Similar habitat segregation has been observed in the Columbia Valley, British Columbia, where Barrow's Goldeneye occurred only on alkaline lakes of plateaus whereas Common Goldeneye were more numerous on freshwater valley lakes (Savard 1984).

We considered nest boxes as a covariate because goldeneyes may use artificial cavities for nesting (Eriksson 1982, Evans et al. 2002, Pöysä and Pöysä 2002) and because boxes were installed on some lakes in our study area in 1998 and 1999 (Savard and Robert 2007) with the intention of studying Barrow's Goldeneye. We believe the relationships between

Barrow's Goldeneye occurrence and nest box presence is partly biased, as we erected nest boxes on lakes which either had pairs or were close to lakes that had pairs of Barrow's Goldeneye during ground surveys conducted in 1998; no nest boxes were established on lakes below 518 m. We used multivariate regression without considering nest boxes and found significant ($P \leq 0.06$) relationships between Barrow's Goldeneye and the exact same variables (i.e., fish occurrence, altitude, interaction of altitude and slope and, depending on data set, number of lakes upstream [all lakes] or riparian wetlands [high elevation lakes]). Coefficients were also similar (0.24 and 0.19, respectively), which supports our conclusion that nest boxes should not be considered as an important variable in this study. Savard (1988) found nest sites up to 2.9 km from pair territories indicating that presence of a nest site (contrary to food resources) was not essential in the selection of a pair territory.

The biological significance of relationships between Barrow's Goldeneye occurrence and other habitat features are less obvious. The mean slope in a 500-m zone radiating from lakes with the low number of lakes upstream may be associated with lake isolation (complete or partial) from fish colonization, increasing invertebrate productivity. It may also be related to cavity availability considering that Barrow's Goldeneye from eastern North America use large, decaying trees for nesting rather than abandoned woodpecker cavities as in western North America (Vaillancourt 2006; MR, unpubl. data). Trees, plus natural rock crevices that could also be used for breeding as in Iceland (Eadie et al. 2000), may be more common around lakes surrounded by mountainous and steep areas, considering that areas ≥4 ha with trees on slopes ≥40% cannot be harvested by the timber industry in Québec (Ministère des Ressources naturelles et de la Faune 2003). Barrow's Goldeneye were also associated with lakes with rocks and cluster of lakes, which may reflect shallow productive waters (Savard et al. 1994, Eadie et al. 2000) and/or provide resting and preening sites (Robert et al. 2006). Barrow's Goldeneye in British Columbia were also associated with lakes that had few riparian marshes or submergent vegetation (Savard et al. 1994, Evans 2003).

A variety of factors may have contributed to the low proportion of variability explained by our models. Our estimate of Barrow's Goldeneye occurrence was based on a single helicopter survey and we may have missed some individuals or observed birds on lakes where they did not breed. Variables such as fish occurrence and the number of lakes upstream probably represent surrogate indicators of lake invertebrate productivity, and actual measures of goldeneye prey availability would probably have yielded better results (Evans 2003). Stocked fishless lakes may remain attractive to goldeneyes for some time as goldeneyes are strongly philopatric (Eadie et al. 2000). Our data set had limitations as most variables used in our analysis were derived from remote sensing and topographic maps. The potentially important variables such as lake depth, availability of nesting cavities, or lake productivity were not considered (Johnson and Winter 2005). These variables were important in lake selection by Barrow's Goldeneye in western North America (Boyd et al. 1989, Savard et al. 1994, Evans 2003). Barrow's Goldeneye is an uncommon species in eastern North America and its population is estimated at <2,000 pairs (Robert and Savard 2006) distributed primarily across Québec's eastern boreal forest during the breeding season (Robert et al. 2000b, 2002). This is a vast area with over 165,000 lakes, >50,000 of which are between 1 and 10 ha in size (NTDB) (Natural Resources Canada 2005). Helicopter surveys conducted yearly from 1990 to 2006 in the central part of the Barrow's Goldeneye breeding area yielded mean pair densities almost 11 times lower for Barrow's Goldeneye than for Common Goldeneye (1.2 vs. 13.0 pairs/100 km^2, respectively) (Daniel Bordage, Canadian Wildlife Service, unpubl. data). The low density and extensive distribution of Barrow's Goldeneye in eastern North America may partly explain the difficulty of predicting its occurrence at the breeding area level even though some variables, such as altitude (Fig. 2) may help in identifying potential breeding areas at the landscape scale.

CONSERVATION IMPLICATIONS

This study has implications for conservation of Barrow's Goldeneye in eastern North

America. It confirms the findings of Robert et al. (2000b) (i.e., Barrow's Goldeneye from eastern North America primarily use high altitudinal, productive lakes during the breeding season) and emphasizes the importance of fishless lakes for that population at risk. Unfortunately, many lakes in our study area have been stocked with brook trout during the last decades ($n \geq 67$, by government agencies alone), especially since logging roads have increased accessibility. The breeding range of Barrow's Goldeneye in Québec covers many areas managed for fishing and hunting activities in which efforts are made to introduce brook trout into originally fishless lakes (Robert et al. 2000a). Stocking of fishless lakes for recreational activities should cease as it may affect Barrow's Goldeneye and have a negative impact on other taxa such as macroinvertebrates and amphibians (Chess et al. 1993, Bradford et al. 1998, Pilliod and Peterson 2001, Drouin et al. 2006). Our study indicates that environmental variables including lake altitude, mean slope, and lake position in the watershed may be useful in predicting Barrow's Goldeneye occurrence at the landscape scale, but not at the lake scale. We believe that management measures should be extended to potential Barrow's Goldeneye breeding areas rather than focussing on lakes with known occurrences, at least until additional, more specific variables can be identified.

ACKNOWLEDGMENTS

This study was funded by the Species at Risk Division of the Canadian Wildlife Service, thanks to Isabelle Ringuet. We sincerely thank Christian Marcotte for participating in helicopter surveys and data compilation. We thank Réjean Benoit for participating in the planning of the helicopter survey as well as the initial data analysis. We are grateful to Hélène Crépeau from Université Laval for data analysis, and Sylvain Deslandes, Marcelle Grenier, and Martine Benoit for GIS analysis. We express our gratitude to Jean Tanguay, from Québec's Ministère des Ressources naturelles et de la Faune, for providing data and information on fishless lakes in our study area. We thank Lise Deschênes, also from Québec's Ministère des Ressources naturelles et de la Faune, for providing details regarding timber harvesting regulations. Michel Melançon kindly produced Figure 1 and calculated the number of lakes distributed within the Barrow's Goldeneye core breeding area. Daniel Bordage kindly provided goldeneye density data from the Waterfowl Survey of Southern Québec Uplands. We also thank Sylvie Gauthier, Stéphane Légaré, Laurent Dufour, and three anonymous reviewers for helpful comments on this paper.

LITERATURE CITED

American Ornithologists' Union (AOU). 1998. Check-list of North American birds. Seventh Edition. American Ornithologists' Union, Washington, D.C., USA.

Bendell, B. E. and D. K. McNicol. 1987. Fish predation, lake acidity and the composition of aquatic insect assemblages. Hydrobiologia 150:193–202.

Bendell, B. E. and D. K. McNicol. 1995. The diet of insectivorous ducklings and the acidification of small Ontario Lakes. Canadian Journal of Zoology 73:2044–2051.

Boyd, W. S. and J.-P. L. Savard. 1987. Abiotic and biotic characteristics of wetlands at Riske Creek, British Columbia: a data report. Technical Report Series Number 16. Canadian Wildlife Service, Delta, British Columbia, Canada.

Boyd, W. S. and D. W. Smith. 1989. Summary of aquatic invertebrate data collected from wetlands at Riske Creek, British Columbia, 1984 and 1985. Technical Report Series Number 60. Canadian Wildlife Service, Delta, British Columbia, Canada.

Boyd, W. S., J.-P. L. Savard, and G. E. J. Smith. 1989. Relationships between aquatic birds and wetland characteristics in the Aspen Parkland, central British Columbia. Technical Report Series Number 70. Canadian Wildlife Service, Delta, British Columbia, Canada.

Bradford, D. F., S. D. Cooper, T. M. Jenkins Jr., K. Kratz, O. Sarnelle, and A. D. Brown. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. Canadian Journal of Fisheries and Aquatic Sciences 55:2478–2491.

Carrara, A. 1988. Drainage and divide networks derived from high-fidelity digital terrain models. Pages 581–597 *in* Proceedings of the NATO Advanced Study Institute on Statistical Treatments for Estimation of Mineral and Energy Resources. D. Reidel Publishing Company, Dordrecht, The Netherlands.

Chess, D. W., F. Gibson, A. T. Scholz, and R. J. White. 1993. The introduction of Lahontan cutthroat trout into a previously fishless lake: feeding habits and effects upon the zooplankton and benthic community. Journal of Freshwater Ecology 8: 215–225.

Cody, R. P. and J. K. Smith. 1997. Applied statistics and the SAS programming language. Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

DesGranges, J.-L. and C. Gagnon. 1994. Duckling response to changes in the trophic web of acidified lakes. Hydrobiologia 279/280:207–221.

Desponts, M. 1996. The biogeography of Québec: major physiographic regions. Pages 18–20 *in* The breeding birds of Québec (J. Gauthier and Y. Au-

bry, Editors). Association québécoise des groupes d'ornithologues, The Province of Québec Society for the Protection of Birds, Société québécoise pour la protection des oiseaux, Canadian Wildlife Service, Environment Canada, Québec Region, Montréal, Canada.

Drouin, A., P. Sirois, and P. Archambault. 2006. Structure des communautés d'invertébrés et des espèces d'amphibiens dans les lacs avec et sans omble de fontaine (*Salvenilus fontinalis*) en forêt boréale. Canadian Technical Report of Fisheries and Aquatic Sciences Number 2628. Institut Maurice-Lamontagne, Mont-Joli, Québec, Canada.

Eadie, J. M. and A. Keast. 1982. Do goldeneye and perch compete for food? Oecologia 55:225–230.

Eadie, J. M., J.-P. L. Savard, and M. L. Mallory. 2000. Barrow's Goldeneye (*Bucephala islandica*). The birds of North America. Number 548.

Einarsson, Á. 1988. Distribution and movements of Barrow's Goldeneye *Bucephala islandica* young in relation to food. Ibis 130:153–163.

Einarsson, Á. 1990. Settlement into breeding habitats by Barrow's Goldeneyes *Bucephala islandica*: evidence for temporary oversaturation of preferred habitat. Ornis Scandinavica 21:7–16.

Einarsson, Á., A. Gardarsson, G. M. Gíslason, and G. Gudbergsson. 2006. Populations of ducks and trout of the River Laxá, Iceland, in relation to variation in food resources. Hydrobiologia 567:183–194.

ENVI. 2005. Environment for visualizing image. RSI Corporate, Boulder, Colorado, USA.

Eriksson, M. O. G. 1979. Competition between freshwater fish and goldeneyes *Bucephala clangula* (L.) for common prey. Oecologia 41:99–107.

Eriksson, M. O. G. 1982. Differences between old and newly established goldeneye *Bucephala clangula* populations. Ornis Fennica 59:13–19.

Evans, M. R. 2003. Breeding habitat selection by Barrow's Goldeneye and Bufflehead in the Cariboo-Chilcotin region of British Columbia: nest sites, brood-rearing habitat, and competition. Dissertation. Simon Fraser University, Burnaby, British Columbia, Canada.

Evans, M. R., D. B. Lank, W. S. Boyd, and F. Cooke. 2002. A comparison of the characteristics and fate of Barrow's Goldeneye and Bufflehead nests in nest boxes and natural cavities. Condor 104:610–619.

Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Gardarsson, A. and Á. Einarsson. 2004. Resource limitation of diving ducks at Myvatn: food limits production. Aquatic Ecology 38:285–295.

Government of Canada. 2007. Species at Risk Act Public Registry. Canadian Wildlife Service, Fisheries and Oceans Canada, and Parks Canada Agency. www.sararegistry.gc.ca/default_e.cfm (accessed 9 January 2007).

Johnson, D. H. and M. Winter. 2005. Planning for bird conservation: a tale of two models. Pages 1205–1212 *in* Bird conservation implementation and integration in the Americas: Proceedings of the Third International Partners in Flight Conference (C. J. Ralph and T. D. Rich, Editors). General Technical Report PSW-GTR-191, USDA, Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Lacasse, S. and P. Magnan. 1994. Distribution postglaciaire de l'omble de fontaine dans le bassin hydrographique du fleuve Saint-Laurent: impact des interventions humaines. Université du Québec à Trois-Rivières, Trois-Rivières, Québec, Canada.

Mallory, M. L., P. J. Blanchard, P. J. Weatherhead, and D. K. McNicol. 1994. Presence or absence of fish as a cue to macroinvertebrate abundance in boreal wetlands. Hydrobiologia 279/280:345–351.

McGarigal, K. and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351, USDA, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Ministère des Ressources naturelles et de la Faune. 2003. Manuel d'aménagement forestier. Gouvernement du Québec, Direction des programmes forestiers, Québec, Québec, Canada.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Natural Resources Canada. 2005. National topographical data base (NTDB). Centre for Topographic Information, Earth Sciences Sector, Natural Resources Canada, Ottawa, Ontario, Canada.

Palmer, R. S. 1976. Handbook of North American birds. Volume 3. Yale University Press, New Haven, Connecticut, USA.

PCI. 2001. EASI PACE Software. Release 6.3 PCI Geomatics Inc., Richmond Hill, Ontario, Canada.

Pilliod, D. S. and C. R. Peterson. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems 4:322–333.

Pope, G. F. and J. C. H. Carter. 1975. Crustacean plankton communities of the Matamek River system and their variation with predation. Journal of the Fisheries Research Board of Canada 32:2530–2534.

Pope, G. F., J. C. H. Carter, and G. Power. 1973. The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density of larvae in the Matamek River system, Québec. Transactions of the American Fisheries Society 4:707–714.

Pope, G., M.-C. Tarissants, J.-F. Frenette, G. Verreault, and J.-L. Desgranges. 1989. Effets des facteurs biotiques et abiotiques sur la structure et les relations trophiques des communautés planctoniques et benthiques: revue des hypothèses. Rapport technique canadien des sciences halieu-

tiques et aquatiques Number 1687. Ministère des Pêches et des Océans, Institut Maurice-Lamontagne, Mont-Joli, Québec, Canada.

PÖYSÄ, H. AND S. PÖYSÄ. 2002. Nest-site limitation and density dependence of reproductive output in the Common Goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. Journal of Applied Ecology 39:502–510.

PÖYSÄ, H. AND J. VIRTANEN. 1994. Habitat selection and survival of Common Goldeneye (*Bucephala clangula*) broods—preliminary results. Hydrobiologia 279/280:289–296.

PÖYSÄ, H., M. RASK, AND P. NUMMI. 1994. Acidification and ecological interactions at the higher trophic levels in small forest lakes: the perch and the Common Goldeneye. Annales Zoologici Fennici 31:397–404.

ROBERT, M. AND J.-P. L. SAVARD. 2006. The St. Lawrence River Estuary and Gulf: a stronghold for Barrow's Goldeneyes wintering in eastern North America. Waterbirds 29:437–450.

ROBERT, M., R. BENOIT, AND J.-P. L. SAVARD. 2000a. Status report on the eastern population of the Barrow's Goldeneye (*Bucephala islandica*) in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ontario, Canada.

ROBERT, M., R. BENOIT, AND J.-P. L. SAVARD. 2002. Relationship among breeding, molting, and wintering areas of male Barrow's Goldeneye in eastern North America. Auk 119:676–684.

ROBERT, M., B. DROLET, AND J.-P. L. SAVARD. 2006. Effects of backpack radio-transmitters on female Barrow's Goldeneyes. Waterbirds 29:115–120.

ROBERT, M., D. BORDAGE, J.-P. L. SAVARD, G. FITZGERALD, AND F. MORNEAU. 2000b. The breeding range of the Barrow's Goldeneye in eastern North America. Wilson Bulletin 112:1–7.

ROBITAILLE, A. AND J.-P. SAUCIER. 1998. Paysages régionaux du Québec méridional. Les Publications du Québec, Sainte-Foy, Québec, Canada.

SAS INSTITUTE INC. 2001. The SAS System for Windows. Release 8.02 TS Level 02MO. SAS Institute Inc., Cary, North Carolina, USA.

SAVARD, J.-P. L. 1984. Territorial behaviour of Common Goldeneye, Barrow's Goldeneye and Bufflehead in areas of sympatry. Ornis Scandinavica 15: 211–216.

SAVARD, J.-P. L. 1988. Winter, spring and summer territoriality in Barrow's Goldeneye: characteristics and benefits. Ornis Scandinavica 19:119–128.

SAVARD, J.-P. L. AND M. ROBERT. 2007. Use of nest boxes by goldeneyes in eastern North America. Wilson Journal of Ornithology 119:28–34.

SAVARD, J.-P. L. AND J. N. M. SMITH. 1987. Interspecific aggression by Barrow's Goldeneye: a descriptive and functional analysis. Behaviour 102: 168–184.

SAVARD, J.-P. L., W. S. BOYD, AND G. E. J. SMITH. 1994. Waterfowl-wetland relationships in the Aspen Parkland of British Columbia: comparison of analytical methods. Hydrobiologia 279/280:309–326.

SÉNÉCHAL, H. 2003. Étude comparative de l'écologie de nidification et d'élevage des couvées de Garrot à œil d'or (*Bucephala clangula*) et de Harle couronné (*Lophodytes cucullatus*) dans un habitat de rivière. Thesis. Université Laval, Québec, Québec, Canada.

TOBISH, T. 1986. Separation of Barrow's and Common goldeneyes in all plumages. Birding 18:17–27.

TOPPING, M. S. AND G. G. E. SCUDDER. 1977. Some physical and chemical features of saline lakes in central British Columbia. Syesis 10:145–166.

VAILLANCOURT, M.-A. 2006. Caractérisation de la disponibilité des arbres potentiels à la nidification du Garrot d'Islande dans la forêt boréale de l'Est du Québec. Thesis. Université du Québec à Montréal, Montréal, Québec, Canada.

VIASAT. 2001. Landsat TM5 satellite imaging, scene identification number: 5013026009915510. Viasat-Géotechnologie Inc., Montréal, Québec, Canada.

WIKEN, E. B. 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series Number 19. Environment Canada, Hull, Québec, Canada.

The Wilson Journal of Ornithology 120(2):331–338, 2008

DISTRIBUTION, ABUNDANCE, AND NEST-SITE CHARACTERISTICS OF BLACK SWIFTS IN THE SOUTHERN ROCKY MOUNTAINS OF COLORADO AND NEW MEXICO

RICHARD G. LEVAD,[1,6] KIM M. POTTER,[2,8] CHRISTOPHER W. SHULTZ,[3] CAROLYN GUNN,[4] AND JOSEPH G. DOERR[5,7]

ABSTRACT.—We surveyed 366 historical and potential nesting sites for Black Swifts (*Cypseloides niger*) from 1997 to 2005 in the Southern Rocky Mountains, evaluated their suitability for nesting, and searched for evidence of occupancy. Our surveys located 70 previously undocumented occupied sites, increasing the inventory of sites in the region from 33 to 103. Our results provide a preliminary estimate of Black Swift population size. Comparison of observed colony sizes with those reported in earlier studies suggests little or no change in population levels over the past 50 years. We rated each nest site on conformance to characteristics described in earlier studies. Analysis of 291 site evaluations support *a priori* assumptions that increasing stream flow, number of potential nest platforms, amount of available moss, shading of potential nest niches, topographic relief of surrounding terrain, and ease of aerial access to potential nest niches contributed to a higher probability the site would be occupied by Black Swifts. *Received 14 March 2007. Accepted 11 September 2007.*

Observers in the late 19th century believed Black Swifts (*Cypseloides niger*) nested in Colorado (Drew 1881, Bendire 1895), but the first breeding confirmation in the Southern Rocky Mountains did not occur until 1949 when O. A. Knorr found nests at two waterfalls near Silverton in San Juan County (Knorr 1950). Knorr searched the mountains of Colorado from 1949 through 1958 for Black Swift colonies and located ~80 nests at 25 sites in 10 counties (Knorr 1953, 1961). In the 38 years (1959–1997) following Knorr's investigations, only seven additional colonies were located in Colorado, six at waterfalls (Bailey and Niedrach 1965; Boyle 1998; Hurtado 2002; Robert Righter, pers. comm.) and one in a limestone resurgence cave (Davis 1964). During this same time period, a single colony was located in the Southern Rocky Mountain Region in northern New Mexico (Johnson 1990).

An ecological pattern emerged from Knorr's investigations leading him to suggest that "five physical factors were found to be present to a greater or lesser degree in all the colonies" (Knorr 1961:167). These five factors included (1) the presence of water—"from a rushing torrent to a mere trickle," (1961:168), (2) high relief—"a commanding position above the surrounding terrain," (1961:168), (3) inaccessibility to terrestrial marauders, (4) darkness—Knorr "never found an occupied nest upon which the sun shone," (1961:168), and (5) unobstructed aerial access—the birds "will not fly through a maze of trees to reach their nests" (1961:168). Later, after evaluating some apparently suitable but unoccupied sites, Knorr added a sixth physical factor of nest sites: the presence of niches in rock for nest placement (Knorr 1993). Subsequent studies have generally concurred with Knorr's analysis of Black Swift nesting characteristics (Hunter and Baldwin 1962, Foerster 1987). The objectives of our paper are to: present (1) the results of extensive investigations of potential Black Swift nest sites in the Southern Rocky Mountains, and (2) a model for predicting Black Swift occupancy based on characteristics of known occupied sites.

METHODS

Field Methods.—The U.S. Forest Service (USFS) designated the Black Swift as a sensi-

[1] Rocky Mountain Bird Observatory, West Office, 337 25 3/4 Road, Grand Junction, CO 81503, USA.

[2] White River National Forest, Rifle Ranger District, 0094 County Road 244, Rifle, CO 81650, USA.

[3] San Juan National Forest, Columbine Ranger District and Field Office, 367 South Pearl Street, Bayfield, CO 81122, USA.

[4] P. O. Box 791, Dolores, CO 81323, USA.

[5] White River National Forest, Eagle Ranger District, P. O. Box 720, Eagle, CO 81631, USA.

[6] Current address: 480 Casey Way, Grand Junction, CO 81504, USA.

[7] Current address: Willamette National Forest, 211 East 7th Avenue, Eugene, OR 97401, USA.

[8] Corresponding author; e-mail: kmpotter@fs.fed.us

TABLE 1. Black Swift surveys in Colorado and northern New Mexico, 1997–2005. Prior to these investigations, 32 colony sites had been located in Colorado and one in New Mexico. Multiple evaluations were conducted at many sites.

State	Year	Sites in data base	New sites surveyed	Total sites surveyed	New colonies found
Colorado	1997	NA	2	4	2
Colorado	1998	NA	41	52	5
Colorado	1999	NA	37	56	5
Colorado	2000	NA	60	106	5
Colorado	2001	311	58	119	21
Colorado	2002	352	76	96	18
Colorado	2003	417	71	149	9
Colorado	2004	426	6	12	3
Colorado	2005	427	1	3	0
Subtotal		427	352	597	68
New Mexico	2003	16	9	9	1
New Mexico	2004	21	7	8	1
Subtotal		21	17	17	2
Totals		448	369	614	70

tive species in the Rocky Mountain Region in 1993 citing the need for more information about its distribution and abundance. The USFS subsequently, in cooperation with the Colorado Natural Heritage Program, canvassed museums and available literature and interviewed knowledgeable individuals to compile an inventory of historically active nest sites, currently active nest sites, potential nest sites, and incidental Black Swift observations. The list of potential nest sites included waterfalls from Conly's *Waterfalls of Colorado* (1993), Burns' *Colorado Ice Climber's Guide* (1997), 7.5-minute USGS topographic maps, and National Forest visitor maps. Surveyors discovered many more potential sites as they traveled to the waterfalls on the initial list.

Field verification began on a small scale in 1997 and, in 1998, the Rocky Mountain Bird Observatory (RMBO) joined USFS and greatly expanded the survey effort (Table 1). From 1998 through 2005, USFS and RMBO personnel and trained volunteers surveyed and evaluated potential Black Swift sites in Colorado. In 2003 and 2004, RMBO, under contract with the New Mexico Department of Game and Fish, conducted surveys in New Mexico. We included sites in northern New Mexico that are within the Southern Rocky Mountain Physiographic Region. We did not conduct any surveys in the small portion of this physiographic region that extends into southern Wyoming.

Surveyors field-tested a Black Swift survey and monitoring protocol during 1998 and 1999 to evaluate it as a status and population trend-monitoring tool. This field protocol, with minor revisions through the course of investigations (Schultz and Levad 2001, 2003), guided our surveys. Surveyors evaluated each site for suitability for Black Swift occupancy using a rating scale based upon, but not identical to, the characteristics described by Knorr (1953, 1961, 1993). Six habitat parameters at each site were individually assigned a numeric rating ranging from 1 to 5 based on increasing abundance or extent (Table 2). The six habitat parameters were: FLOW (the amount of flowing surface water during late summer), RELIEF (the extent of relief or prominence over surrounding terrain from the top of the site), ACCESS (the extent of aerial access to or from the nest niches), SHADING (the extent of shading of nest niches), NICHES (the number of suitable nest niches inaccessible to ground predators), and MOSS (the amount of moss available at the nest site). We conducted an intensive training session for surveyors each year to standardize interpretation of the subjective descriptors of nest site characteristics.

Surveyors searched each potential site for nests and other evidence of Black Swift occupancy, such as the presence of urates. They recorded the maximum number of adult swifts seen simultaneously flying about or roosting at the site to develop an estimate of minimum colony size. Observers remained at the site until dark when feasible to detect and/or count adults arriving to roost.

Sites were rated as occupied if any of three conditions were met: (1) a nest containing an incubating Black Swift adult, egg, or chick was observed; (2) a used Black Swift nest was observed; or (3) Black Swifts were observed coming to roost at a suitable nest location. We cautiously applied the second criteria because Cordilleran Flycatcher (*Empidonax occidentalis*) and Townsend's Solitaire (*Myadestes townsendi*) nests can be confused with those of Black Swifts. Nests of these three species were distinguished by structure, placement, and materials. The third criterion does not meet the standard for confirmation of nesting for most species, but we designated these sites

TABLE 2. Rating scale for Black Swift colony site characteristics.

	1	2	3	4	5
FLOW	None	Weak	Moderate little spray	Moderate much spray	Heavy
RELIEF	Falls at bottom of terrain	Little view from top of falls	Moderate view from top of falls	Good view from top of falls	Commanding view from top of falls
ACCESS	No clear access	Access clear to ¼ of niches	Access clear to ½ of niches	Access clear to ¾ of niches	Access clear to all niches
SHADING	Nest niches sunlit all day	Sunlit >3 hrs/day	Sunlit 1–3 hrs/day	Sunlit <1 hr/day	Shaded all day
NICHES	No suitable niches present	Few niches and/or all niches accessible	Some niches and most niches accessible	Some niches and most niches inaccessible	Many niches and most niches inaccessible
MOSS	No moss	Trace of moss	Scattered moss	Frequent moss	Abundant moss

as occupied because there is no confirmed record of Black Swifts roosting during the breeding season at a site where nests were not present (Lowther and Collins 2002; O. A. Knorr, pers. comm.). "Occupied" thus does not absolutely indicate that nests are present; but that Black Swifts use the site and the probability of nests being present is extremely high. We designated as occupied all sites that had been found to meet any of these criteria, whether that finding was made in the current study or by earlier observations.

We considered sites vacant when one or more surveys were completed and no birds or swift nests were detected. We considered a survey completed when all potential nest niches were examined or when an evening watch was conducted. Sites were rated as occupancy unknown when it was not possible to examine all potential nest niches and when an evening watch was not conducted.

Data Analysis.—The variables FLOW, RELIEF, ACCESS, SHADING, NICHES, and MOSS were used to develop a model to predict Black Swift occupancy at 291 sites using "all-subsets selection" binary logistic regression analysis and the Akaike information-theorectic approach (Burnham and Anderson 2002). These authors have stressed that an informed selection of independent variables is critical to meaningful model inferences. We based our model on the variables outlined by Knorr (1953, 1961, 1993) and followed by Hunter and Baldwin (1962) and Foerester (1987). We combined two of Knorr's criteria—presence of niches and their accessibility by ground predators—because we were evaluating potential as well as actual nest sites. We added moss availability as a characteristic for evaluation because all nests in the Southern Rockies up to this time have been constructed of moss (Lowther and Collins 2002). The six variables we used in our model were weakly correlated with each other (r values $<$ 0.55). Wald Chi-square was used to test the significance of each predicting variable (Kleinbaum 1994). Logistic regression calculations were performed using SAS Enterprise Guide software (SAS Institute 2001).

RESULTS

We compiled a catalog of 427 potential Black Swift nesting sites in Colorado and an

additional 21 sites in northern New Mexico by the end of the 2005 field season. We completed 597 visits at 352 sites in Colorado and an additional 21 visits at 17 sites in northern New Mexico (Fig. 1). Some sites in both Colorado and New Mexico were visited more than once, and each visit generated an evaluation form.

We confirmed occupancy by Black Swifts in at least 1 year at 96 sites in Colorado and three sites in New Mexico. We located 68 new nest sites in Colorado and two new sites in New Mexico during the course of this study. We located active nests at 58 of the new sites and observed adults coming to roost at the remaining 12.

Binary logistic regressions for the dependent variable OCCUPIED were calculated for 63 combinations of the predicting variables FLOW, RELIEF, ACCESS, SHADING, NICHES, and MOSS, plus the intercept-only (null) model, and evaluated for best fit using Akaike's Information Criterion (AIC). Variance inflation factors for the six-predictor variables ranged from 1.15 to 1.98. Multicollinearity was not a concern with the models. Only two candidate models had ΔAIC <10 of the best model (Table 3). Generalized R^2 for the three top candidate models ranged from 0.596 to 0.610, in order of decreasing AIC value. The global model was the best model and accounted for 93% of the Akaike weights in the all-subset evaluation of the six variables. Given the 291 sample sites, the best model was approximately 10^{56} times more likely to be the correct model than the intercept-only model. The importance values were 1.0 for RELIEF, ACCESS, SHADING, and NICHES, and 0.98 and 0.95 for FLOW and MOSS, respectively. The equation for the best model was:

$$P_i = 1/(1 + e^{-z}),$$

where P_i = the probability of Black Swifts not being detected at site i and

$$\begin{aligned} z_i = 30.664 &- (0.760 \times \text{FLOW}_i) \\ &- (1.225 \times \text{RELIEF}_i) \\ &- (2.123 \times \text{ACCESS}_i) \\ &- (1.534 \times \text{SHADING}_i) \\ &- (1.596 \times \text{NICHES}_i) \\ &- (0.947 \times \text{MOSS}_i). \end{aligned}$$

Each predicting variable was significantly different from zero ($P < 0.01$). The best model correctly predicted occupancy for 95% of the original sites ($n = 291$) that were used to build the model (Table 3).

DISCUSSION

Knorr's decade of work extended the known geographical distribution of Black Swifts breeding in Colorado from the San Juan Mountains in the southwestern part of the state north to the White River Plateau and Rocky Mountain National Park, and east to the eastern flank of the Sangre de Cristo Mountains (Knorr 1953, 1961). Our study only slightly changed the overall distribution from what Knorr described. The discovery of a colony site on the West Fork of the Elk River in Routt County, Colorado, made the greatest expansion, extending the known range in the Southern Rocky Mountains ~65 km northward.

Occupied swift sites are not uniformly distributed across the region (Fig. 1) because locations of waterfalls are not uniform. Three geographic areas contained a high percentage of the occupied sites visited during our study: the San Juan Mountains in southwestern Colorado, Rocky Mountain National Park in northern Colorado, and the White River Plateau in central Colorado. We found that occupied sites often occur in relatively close proximity, forming groups of 4–10 sites that are likely well within the daily foraging distance of adults (Lowther and Collins 2002). This apparent clustering suggests swifts from neighboring sites may interact and groups of occupied sites may form core areas that could contribute to swift population dynamics and broad-scale population persistence. Research into the meta-population dynamics and extent of relatedness in these groups would be informative.

Our study slightly extended the elevation range for Black Swift colonies in the Southern Rocky Mountains. Prior to this study, the elevation of known colonies ranged from 2,195 to 3,505 m. We found sites that ranged in elevation from 2,024 to 3,560 m, with only two sites lower and one higher than the range of earlier sites. The mean elevation of all currently known Southern Rocky Mountain Black Swift colonies is 3,035 m.

Most (93%) of the occupied nest sites vis-

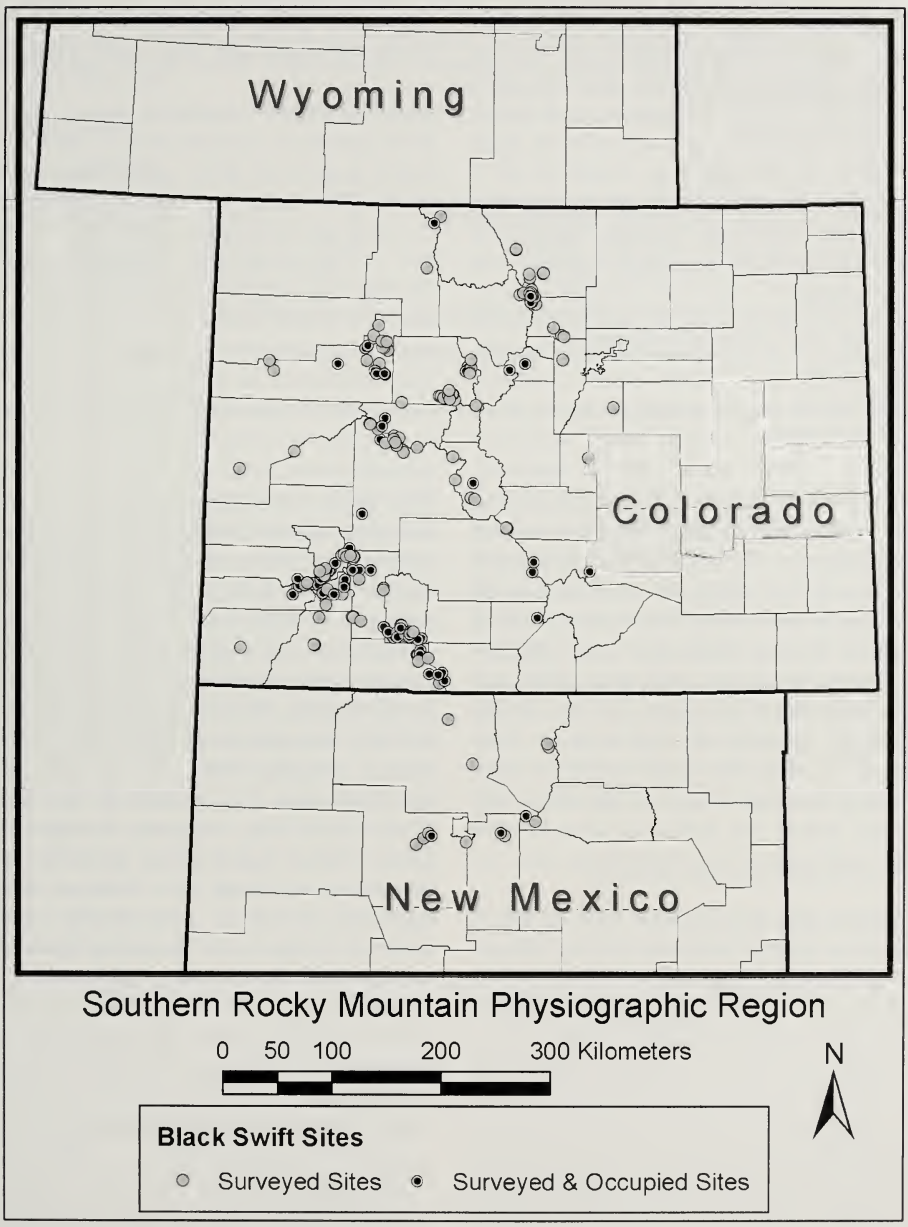


FIG 1. Sites surveyed and occupied by Black Swifts in the Southern Rocky Mountains, 1997–2005.

ited were at waterfalls with drops ranging from 5 to more than 100 m. Five sites were unusual in that colonies occupied shallow caves or drippy alcoves. Of these five sites, four are within 200–400 m of occupied waterfalls and each supports only one or two pairs of swifts. The most unusual site is a large colony nesting in a resurgence cave where up to nine pairs of swifts nest as much as 23 m from the cave entrance.

Black Swifts are known to have strong fidelity to their nesting sites (Collins and Foerster 1995, Lowther and Collins 2002), a characteristic that was further corroborated by our study. We believe we located 24 of the 25 sites Knorr found in Colorado in the 1950s

TABLE 3. Binary logistic regression models for detecting Black Swifts at waterfall sites in Colorado and northern New Mexico evaluated with Akaike's Information Criterion (AIC). Shown are the intercept-only (null) model and all candidate models with ΔAIC[a] values <10.

Model terms[c]	ΔAIC	w[d]	Correct predictions, %[b]	
			Unoccupied sites (n = 191)	Occupied sites (n = 100)
FLOW, RELIEF, ACCESS, SHADING, NICHES, MOSS	0	0.928	96.3 (87.4)	91.0 (77.0)
RELIEF, ACCESS, SHADING, NICHES, MOSS	5.74	0.053	95.8 (85.9)	91.0 (72.0)
FLOW, RELIEF, ACCESS, SHADING, NICHES	7.814	0.019	94.8 (85.3)	90.0 (70.0)
Null (intercept only)	261.785	10^{-57}		

[a] Difference in AIC values compared to the best model.
[b] A correct prediction is a site that is correctly identified as occupied or unoccupied with a probability > 0.50. In parentheses is the percent of correct predictions with $P > 0.80$.
[c] Model terms are in text.
[d] Akaike weight (Burnham and Anderson 2002). The ratio of w_a/w_b shows the odds that Model a is better than Model b, given the independent variables and data set selected for testing.

although there is some uncertainty concerning the location of a few of those sites due to lack of documentation. We confirmed continued occupancy at 23 of these 24 sites nearly 50 years after their discovery. We surveyed all of the Southern Rocky Mountain sites discovered by others between 1950 and 1996 and confirmed continued occupancy at five of the seven sites in Colorado as well as at the lone site in New Mexico. We were unable to conduct evening watches at any of the three historical sites where we failed to detect swift occupancy and cannot conclude these sites are vacant.

The historically documented size of Black Swift colonies in the Southern Rocky Mountains ranges from a single pair to 18 pairs. The largest known colony, averaging 11 active nests, is in Box Canyon Falls in Ouray County, Colorado, a site that was discovered by Knorr in 1950. Some small colonies of one or two nests appear to be intermittently occupied, but larger colonies seem to be occupied annually and to remain relatively stable in size.

Our surveys produced an estimate of 2.5 pairs per occupied site based on counts of adults and nests. If those counts are accurate, the total Black Swift breeding population at documented occupied sites in the Southern Rocky Mountains (n = 103) is ~500 breeding adults. If the rate of occupancy at presently identified potential sites that have not yet been surveyed (n = 58) is similar to those that have already been surveyed, those sites may support an additional 75 breeding adults. If our model is accurate in predicting occupancy at sites where surveys were inconclusive (n = 76), those sites could support another 300 breeding adults. Although our catalog of potential nest sites contains all published and mapped waterfalls in the region, our field experience indicates there are a number of potential sites that appear neither in publications nor on maps. A review of topographical maps in the region, focusing on permanent steams flowing through steep gradients, produced estimates ranging from 105 to 420 additional potential sites that remain to be catalogued. These sites may support another 200–750 birds. These calculations produce an upper population estimate of ~1,000–1,600 breeding birds, which is quite similar to the estimate of 1,400–1,600 breeding birds in Colorado provided by Boyle (1998).

Our analysis of the six habitat characteristics at Black Swift nesting sites supports Knorr's conclusions about their relationship to swift occupancy. Some of these characteristics may be by-products of nest site selection rather than nesting requirements (Marín and Stiles 1992, Marín 1997). Our most parsimonious model supported the *a priori* assumptions that volume of stream flow, number of potential nest platforms, amount of moss cover, extent of shading of potential nest platforms, extent of topographic relief, and ease of aerial access to the potential nest sites each significantly contributed to a higher probability the site would be occupied by Black Swifts. Discussion of nest requirements by Marín (1997) suggests a simpler model using only FLOW and NICHES. This model correctly predicted occupancy for 84.2% of the sites in our study. The Akaike weights suggest the global model

was about 10^{21} times more likely to be the correct model than this two-variable model based on our data set.

The best model predicted that three occupied sites had <20% chance of being used. These are small sites, each hosting a single nest. Occupancy at one site appears to be intermittent and the other two were the only occupied sites that received a rating of "2" (of a maximum possible score of "5") for NICHES. All three sites have other, larger colonies nearby and may represent sub-optimal habitat sites occupied only when all available nest niches at the primary sites are in use. It is possible that some similar sites we counted as unoccupied are actually used intermittently and we failed to detect empty nest structures.

Black Swift nest site selection provides several advantages. The inaccessibility of nest niches makes nests and eggs nearly invulnerable to terrestrial predation. This low predation rate enables relatively high nest success (72%; Hirshman et al. 2007) and maintenance of population stability (Hunter and Baldwin 1962, Foerester 1987, Lowther and Collins 2002, Hirshman et al, 2007) despite a relatively low reproductive rate (1 egg/clutch and 1 clutch/year). Temperature parameters have not been measured at the nest, but the shaded, damp sites are cool and likely have minimal temperature fluctuation. These factors may slow the metabolism of nestlings and permit adults to leave them unattended for long periods during their wide-ranging foraging flights (Lowther and Collins 2002). The high relief above surrounding terrain typical of most nest sites enables adults to reach high altitudes at which they forage quickly and with little effort.

CONSERVATION IMPLICATIONS

A common but largely untested hypothesis in avian ecology is that animals tend to select habitats that increase fitness, survival, and reproductive success. Our best model predicted that <2% of the 191 waterfalls where we failed to detect Black Swifts had a greater than 80% probability of occupancy. If the sites sampled in our study are representative of all potential sites in the region, our model results suggest that most of the highest quality swift nesting habitat is already occupied, and population size of Black Swifts may be limited by suitable nesting habitat. Locating and protecting the limited number of suitable nesting sites that are currently available, and identifying their occupancy status, should remain a high priority for conservation of this species.

In Colorado, low population numbers have resulted in the Black Swift being designated a sensitive species on National Forest lands and listed as a vulnerable breeder by the Colorado Natural Heritage Program. The U.S. Forest Service clearly carries the greatest conservation responsibility for this species in the Southern Rocky Mountains. Within Colorado, 73% of all occupied Black Swift sites are on National Forest lands. Colorado's San Juan National Forest hosts 26% of the state's known occupied sites while the White River National Forest and Uncompahgre National Forest each host 18%. Two of the three confirmed sites in New Mexico are on National Forest lands. Our model should be helpful for identifying which sites are most likely to provide nesting habitat and for prioritizing survey efforts among sites where occupancy has not been ascertained. Our field survey protocol appears to be effective and the model predicts the probability of site occupancy with confidence.

ACKNOWLEDGMENTS

Colorado data for this study were collected through the Rocky Mountain Bird Observatory's *Monitoring Colorado's Birds* program, which is supported by the Colorado Division of Wildlife, U.S. Forest Service, Bureau of Land Management, and National Park Service. The Rocky Mountain Bird Observatory collected New Mexico data under contract with the New Mexico Department of Fish and Game. David Khaliqi provided early assistance with statistical analysis. Data were collected by 78 field technicians and volunteers; the authors especially thank J. P. Beason and K. D. Behrens for many days of field work, and arduous hiking and climbing, as well as for providing insights and advice on the manuscript. The authors thank Allison Cariveau and J. R. Young for reviewing earlier drafts of the manuscript; their careful reading and suggestions were invaluable.

LITERATURE CITED

Bailey, A. M. and R. J. Niedrach. 1965. Birds of Colorado. Volume 2. Denver Museum of Natural History, Denver, Colorado, USA.

Bendire, C. 1895. Life histories of North American birds. U.S. National Museum Special Bulletin 3: 175–177.

Boyle, S. 1998. Black Swift (*Cypseloides niger*). Pag-

es 236–237 *in* Colorado breeding bird Atlas (H. E. Kingery, Editor). Colorado Bird Atlas Partnership and Colorado Division of Wildlife, Denver, USA.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, USA.

Burns, C. M. 1997. Colorado ice climber's guide. Chockstone Press Inc., Evergreen, Colorado, USA.

Collins, C. T. and K. S. Foerster. 1995. Nest site fidelity and adult longevity in the Black Swift (*Cypseloides niger*). North American Bird Bander 20:11–14.

Conly, M. 1993. Waterfalls of Colorado. Pruett Publishing Company, Boulder, Colorado, USA.

Davis, D. G. 1964. Black Swifts nesting in limestone cave in Colorado. Wilson Bulletin 76:295–296.

Drew, F. M. 1881. On the birds of San Juan County, Colorado. Bulletin of the Nuttall's Ornithological Club 6:127–148.

Foerster, K. S. 1987. The distribution and breeding biology of the Black Swift (*Cypseloides niger*) in southern California. Thesis, California State University, Long Beach, USA.

Hirshman, S. E., C. Gunn, and R. G. Levad. 2007. Breeding phenology and success of Black Swifts in Box Canyon, Ouray, Colorado. Wilson Journal of Ornithology 119:678–685.

Hunter, J. E. and P. H. Baldwin. 1962. Nesting of the Black Swift in Montana. Wilson Bulletin 74: 409–416.

Hurtado, P. 2002. Probable Black Swift (*Cypseloides niger*) nesting colony in the Wet Mountains, Pueblo County. Journal of the Colorado Field Ornithologists 36:60–61.

Johnson, P. W. 1990. Black Swift (*Cypseloides niger*) nesting in the Jemez Mountains of New Mexico. New Mexico Ornithological Society Bulletin 18: 13–15.

Kleinbaum, D. G. 1994. Logistic regression: a self-learning text. Springer-Verlag, New York, USA.

Knorr, O. A. 1950. First breeding record of the Black Swift (*Nephoecetes n, borealis*) in Colorado. Auk 67:516.

Knorr, O. A. 1953. The geographical and ecological distribution of the Northern Black Swift in Colorado. Thesis, University of Colorado. Boulder, USA.

Knorr, O. A. 1961. The geographical and ecological distribution of the Black Swift in Colorado. Wilson Bulletin 73:155–170.

Knorr, O. A. 1993. Black Swift nesting site characteristics: some new insights. Avocetta 17:139–140.

Lowther, P. E. and C. T. Collins. 2002. Black Swift (*Cypseloides niger*). The birds of North America. Number 676.

SAS Institute. 2001. SAS enterprise guide. Version 8. Second Edition. Cary, North Carolina, USA.

Marín, M. 1997. Some aspects of the breeding biology of the Black Swift Wilson Bulletin 109:290–306.

Marín, M. and F. G. Stiles. 1992. On the biology of five species of swifts (*Apodidae, Cypseloidinae*) in Puerto Rico. Proceedings Western Foundation of Vertebrate Zoology. 4:287–351.

Schultz, C. and R. Levad. 2001. Black Swift monitoring protocol. Unpublished report. USDA, Forest Service, San Juan National Forest, Bayfield, Colorado, USA.

Schultz, C. and R. Levad. 2003. Black Swift monitoring protocol. Unpublished report. USDA, Forest Service, San Juan National Forest, Bayfield, Colorado, USA.

The Wilson Journal of Ornithology 120(2):339–344, 2008

NEST REUSE BY VERMILION FLYCATCHERS IN TEXAS

KEVIN S. ELLISON[1,2]

ABSTRACT.—Vermilion Flycatchers (*Pyrocephalus rubinus*) were documented to reuse their nests within a single breeding season in south Texas. I recorded a consistent, low frequency (12%, $n = 250$ clutches) of nest reuse during each of four seasons. Nest survival was greater ($P < 0.001$) for reused nests than for newly constructed nests and the abundance of ectoparasites was low overall for both types of nests. The main advantage for Vermilion Flycatchers reusing nests was greater nesting success as nest reuse was associated with reduced nest predation. Nest reuse also increased time available for nesting attempts as a flycatcher would save 8 days (9%) (during three attempts) of the time typically available for nesting in south Texas. Reported nest reuse was common (>25% of a family's members) among 5 families of passerines. Aspects of the life histories of these groups support hypotheses for the observed nest reuse behavior among Vermilion Flycatchers. *Received 3 February 2007. Accepted 29 September 2007.*

Most passerine birds construct a new nest for each breeding attempt despite the potential for reusing their own nests. Strategies of nest construction or reuse differ in costs as construction of new nests requires time and energy. Reuse of nests or nest sites can be associated with costs such as greater exposure to ectoparasites (Møller 1994, Brown and Brown 1996, Møller and Erritzøe 1996, Stanback and Dervan 2001), predators (Styrsky 2005, Yeh et al. 2007) or adverse microclimates (e.g., where conditions differ since time of construction). Most studies of nest reuse have focused on birds that use stable and/or complex nesting structures (Lindell 1996) with an emphasis on reuse of nesting structures between years (Barclay 1988, Cavitt et al. 1999, but see Styrsky 2005).

My objectives were to: (1) compare the success of reused and newly constructed nests of Vermilion Flycatchers (*Pyrocephalus rubinus*), and (2) explore whether ectoparasites affected nest reuse. I also reviewed the literature on nest reuse within a single season to examine the relative frequency of this behavior and to identify characters associated with nest reuse (e.g., complex nest structures, habitats, etc.).

METHODS

Study Site.—I monitored 250 Vermilion Flycatcher nests at Fort Clark Springs, a private residential community in Kinney County, Texas (29° 18′ N, 100° 43′ W) during 1999–2002. The site consists of manicured lawns, huisache (*Acacia minuata*), and honey mesquite (*Prosopis glandulosa*), as well as riparian woodland of pecan (*Carya illinoensis*) and live oak (*Quercus virginiana*).

Field Methods.—Nests were located systematically by searching a 40-ha area with the entire area searched approximately every 3 days. Success of nest searching was calibrated with bi-weekly spot map censuses (IBCC 1970) of all birds within a 27-ha subset of the area. This method allowed targeting territories of males for which a nest had not been located as well as facilitated accurate estimation of densities of singing males and nesting pairs.

Nest Monitoring.—Each Vermilion Flycatcher nest was checked daily until the end of laying after which nest checks were at 1–4 day intervals. Nests were checked from the ground with a mirror attached to an extendable pole or from a ladder. Birds were not banded and I could not directly identify whether nest reuse involved the birds that constructed the nest. Thus, I relied upon detailed, bi-weekly spot-maps of songbird territories (IBCC 1970) and egg laying dates to examine the likelihood the same female reused the nest. I used the difference of the earliest and latest first egg dates for each season to estimate breeding season length. I calculated the interval between nest attempts, for reused nests, as the difference between the date of fledging and the first egg date of the subsequent clutch. I excluded data for two reused nests in 2000 because a second attempt may

[1] Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada.

[2] Current address: Department of Forest and Wildlife Ecology, 1630 Linden Drive, University of Wisconsin, Madison, WI 53706, USA; e-mail: ksellison@wisc.edu

have been missed; the intervals were 38–45 days. I also excluded data from third attempts ($n = 3$) using the same nest.

Daily probability for nesting success at the egg and nestling stages was calculated using the Mayfield (1975) method with the Hensler and Nichols (1981) correction. Nest success rates for each nesting strategy (reuse vs. new nest) were compared using nest data from all 4 years and program CONTRAST (Hines and Sauer 1989). Nests reused more than once were considered as independent data points for reuse. I also compared clutch sizes of reused and new nests to identify any tradeoff with construction and egg production.

A random sample of nests was examined for ectoparasites or their presence (e.g., puparia or eggs). Nests were collected 2–5 days after they became inactive. Twenty-one nests were collected; four which had been reused and 17 new nests. Three of the reused nests had been successful and one failed at the egg stage. One of the new nests failed at the egg stage, two failed at the nestling stage, and 14 were successful. Each nest was sealed in a plastic bag upon collection and frozen until the contents were examined in the laboratory. Each bag was weighed before disassembling each nest in a Petri dish. A 320X dissecting scope was used to scan all nest materials and contents. Nest materials were separated by categories of twigs, feathers, grass, and moss/lichen. Voucher specimens of all arthropod materials were collected and preserved in ethanol. Specimens were identified to Order and/or Family by T. A. Galloway, Department of Entomology, University of Manitoba, Winnipeg. Nest mass was compared between reused and new nests to ascertain whether reused nests were larger.

Literature Review.—The relative frequency of nest reuse among passerine bird families was examined by surveying the literature for records of nest reuse. Both the "Nesting-reuse of old nests" section in The Birds of North America series (1999–2002, Volumes 1–18) and the Searchable Ornithological Research Archive (SORA) website (http://elibrary.unm.edu/sora) were searched. Analysis by bird families was limited to those with two or more species common to North America and considered only species that build open-cupped nests. Species were excluded for which adequate (>20 nests) published nesting data did not exist.

RESULTS

Vermilion Flycatchers reused nests, presumably their own, which had been successful that season for 12% of reproductive attempts ($n = 250$ clutches). I recorded the ultimate fate for 27 of these attempts; 19 were successful and 8 failed due to predation.

Vermilion Flycatchers laid eggs shortly after young from a previous brood fledged at 26 nests (3 nests were used 3 times). First egg dates ranged from 1 April to 17 July; mean (± SE) breeding season length was 94.0 ± 6.6 days ($n = 3$). The mean span was 6.6 ± 3.3 days at the 25 reused nests where the length between fledging and the first egg of the next clutch was known. Detailed maps of territories and comparison of laying dates suggested nests were reused by the same females that constructed the first nests. No nests were known to be used between years and nests from the previous year were not found.

The daily survival rate for reused nests was higher ($\chi^2_1 = 30.49$, $P < 0.001$) than for those newly constructed (Fig. 1). Nest failure was primarily due to predation (98%, 47 nests of known fate) as brood parasitism was infrequent (3% of 250 nests were parasitized by Brown-headed Cowbirds [*Molothrus ater*]). Clutch size ($\bar{x}$ ± SE) did not vary between seasons among nests used once (1999: 3.07 ± 0.73 eggs, $n = 14$, range = 2–5; 2000: 2.95 ± 0.50 eggs, $n = 41$, range = 2–5; 2001: 3.10 ± 0.54 eggs, $n = 51$, range = 2–4; 2002: 2.93 ± 0.37 eggs, $n = 29$, range = 2–4; Kruskal-Wallace $\chi^2_3 = 3.59$, $P = 0.31$). Mean clutch size did not differ between nests used once and those used again (Mann-Whitney $U_{14,135} = 891.50$, $P = 0.63$). Three of the 17 reused nests where clutch size was known contained larger subsequent clutches.

There was little evidence of activity of ectoparasites in the 21 nests I examined. One nest was infested by mites (>2,500 individuals, *Dermanyssus* spp.) and three nests contained single Dipteran puparia. The mite-infested nest fledged at least three young. Both nests that failed at the egg stage contained no arthropods. Mite infestation (>500 mites) was detected at one Vermilion Flycatcher nest during nest monitoring. Neither nest success nor

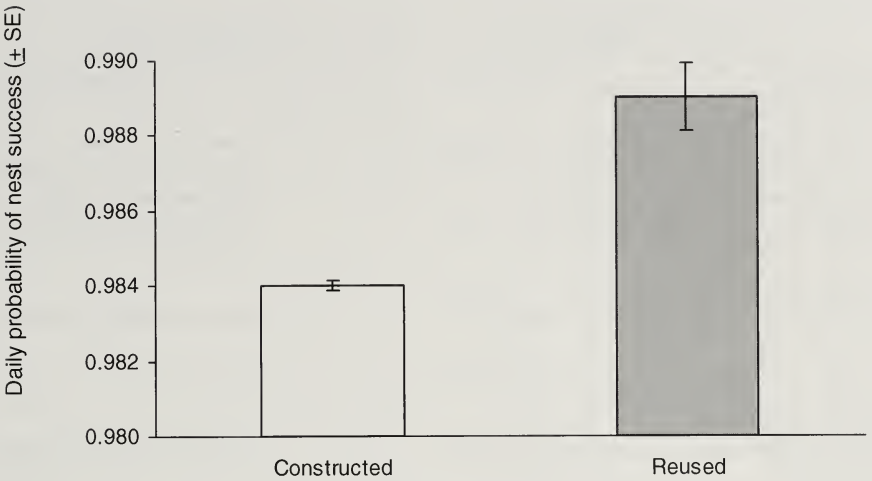


FIG.1. Nest success for the sub-sample of Vermilion Flycatcher nests for which the necessary data were available: 214 constructed and 24 reused nests.

nest reuse was associated with nest mass (r_s = 0.09, P = 0.72, n = 20; $U_{4,16}$ = 19.00, P = 0.22).

Nest reuse, based on a review of the literature, was most frequent among the Tyrannidae (5 species), Emberizidae (7 species), and Icteridae (6 species). Nest reuse relative to the number of species per family only occurred among >25% of members of the: Lanidae (50%, n = 2), Turdidae (33%, n = 10), Mimidae (33%, n = 10), Bombycilidae (50%, n = 2), and Icteridae (30% of 20 spp.) (Table 1).

DISCUSSION

Twenty-nine (12%) of 250 Vermilion Flycatcher clutches were in reused nests during the same season the nests were constructed. Nest reuse by this species had not been recorded previously (Wolf and Jones 2000:10). Reused nests fared better than those newly constructed. Only successful nests were reused and there was little evidence for costs associated with ectoparasites at reused nests. Reuse apparently offers a benefit of time for producing more young and nests were reused up to three times per season. Vermilion Flycatcher nests require a minimum of 4 days for construction (K. S. Ellison, unpubl. data). Thus, nest reuse saves at least 4 days per nest attempt; a total savings of 8 days (8–9% of a typical breeding season) when attempting three clutches. Any benefit of time savings would fluctuate between years, as breeding season length generally reflects rainfall, which is extremely variable (±5 to 6 on the Palmer Drought Severity Index, 1698–1980) in south Texas (Stahle and Cleavland 1988). This could be important as the Vermilion Flycatcher has been suspected of being double-brooded (Wolf and Jones 2000).

The habitat suitability hypothesis (Fretwell and Lucas 1969) predicts that fecundity should be greater in the central area of a species range. Texas represents the northeastern extent of breeding for the Vermilion Flycatcher (Wolf and Jones 2000). Thus, nest reuse in Texas may reflect greater selection for more nesting attempts than elsewhere. Limited nesting data from Argentina in the central portion of the Vermilion Flycatcher breeding range suggest that daily nest survival is lower (0.932, n = 23 nests) (Mason 1985). More complete fecundity data, particularly those incorporating breeding season length and number of renesting attempts by individuals, are required to fully test this hypothesis. Regional comparisons of data for reuse of nest materials for construction of new nests (Taylor and Hanson 1970, Carothers 1974) may clarify factors influencing renesting.

Nest reuse, although rare among open cup nesting passerines (Clark and Mason 1985), is more common among the Lanidae, Turdidae, Mimidae, Bombycillidae, and Icteridae than for most other avian families in North America (Table 1). Shrikes and waxwings stand out

TABLE 1. Species reported reusing nests within a breeding season.

Family/Common name	Scientific name	Reference(s)
Tyrannidae (27 species)		
Western Wood-Pewee	*Contopus sordidulus*	(Curson et al. 1996)
Acadian Flycatcher	*Empidonax virescens*	(Whitehead and Taylor 2002)
Willow Flycatcher	*E. traillii*	(Yard and Brown 1999)
Least Flycatcher	*E. minimus*	(Briskie and Sealy 1988)
Vermilion Flycatcher	*Pyrocephalus rubinus*	This paper
Laniidae (2 species)		
Loggerhead Shrike	*Lanius ludovicianus*	(Grimes in Bent 1950:135)
Corvidae (19 species)		
Mexican Jay	*Aphelocoma ultramarina*	(Brown 1994)
Polioptilidae (4 species)		
Black-tailed Gnatcatcher	*Polioptila melanura*	(Farquhar and Ritchie 2002)
Turdidae (10 species)		
Northern Wheatear	*Oenanthe oenanthe*	(Kren and Zoerb 1997)
Townsend's Solitaire	*Myadestes townsendi*	(Bowen 1997)
Wood Thrush	*Hylocichla mustelina*	(Friesen et al. 1999)
Mimidae (10 species)		
Bendire's Thrasher	*Toxostoma bendirei*	(Gilman 1915)
Curve-billed Thrasher	*T. curvirostre*	(Gilman 1909)
Le Conte's Thrasher	*T. lecontei*	(Sheppard 1996)
Bombycillidae (2 species)		
Cedar Waxwing	*Bombycilla cedrorum*	(Mountjoy and Robertson 1988)
Parulidae (51 species)		
Hooded Warbler	*Wilsonia citrina*	(L. J. Petit, unpubl. data)
Emberizidae (49 species)		
Spotted Towhee	*Pipilo maculatus*	(Greenlaw 1996)
California Towhee	*P. crissalis*	(Kunzmann et al. 2002)
Field Sparrow	*Spizella pusilla*	(Allaire 1972, Nicholson 1981)
Lark Sparrow	*Chondestes grammacus*	(McNair 1984, 1985; K. S. Ellison, unpubl. data)
Dark-eyed Junco	*Junco hyemalis*	(Nolan et al. 2002, Yeh et al. 2007)
Song Sparrow	*Melospiza melodia*	(Nice 1937)
Painted Bunting	*Passerina ciris*	(Lowther et al. 1999)
Icteridae (20 species)		
Red-winged Blackbird	*Agelaius phoeniceus*	(Harms et al. 1991)
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	(Harms et al. 1991)
Boat-tailed Grackle	*Quiscalus major*	(Bancroft 1987)
Great-tailed Grackle	*Q. mexicanus*	(Peer and Sealy 2000)
Hooded Oriole	*Icterus cucullatus*	(K. S. Ellison, unpubl. data)
Scott's Oriole	*I. parisorum*	(Flood 2002)
Fringillidae (16 species)		
House Finch	*Carpodacus mexicanus*	(van Riper 1976, Hill 1993)
Evening Grosbeak	*Coccothraustes vespertinus*	(Gillihan and Byers 2001)

among these groups due to their diets and prevalence at relative high latitudes. Both factors can restrict breeding season length and increase selection for nest reuse. Nest reuse among Icteridae was rare relative to sampling effort (Harms et al. 1991) when compared to Tyrannidae and Mimidae. However, few published studies present data on frequency of nest reuse and it is difficult to assess the number of studies that lacked the capability to de-

tect reuse. I suggest that nest reuse is more common than recorded, especially for the Tyrannidae. Members of this group differ little in behavior and it is likely that closely related species also reuse nests. For instance, three species of *Empidonax* flycatchers occasionally reuse their nests suggesting this behavior may occur throughout the genus.

Nest building may be costly for females in terms of time and energy that could otherwise be devoted to egg production and provisioning (Conrad and Robertson 1993). Cavitt et al. (1999) assessed between-season nest reuse by Brown Thrashers (*Toxostoma rufum*) and found those reusing nests saved 3–8 days of nest construction. Few data exist on the energetic demands of nest construction among open-cup nesting songbirds (Biedenneg 1983). However, most species likely expend far less energy building nests than for incubation or rearing young (Weathers 1992, 2001). Biedenneg (1983) reported that Northern Mockingbirds (*Mimus polyglottos*) did not elevate their energy expenditures during nest building relative to other reproductive stages (pre-building, incubating, etc.). I conclude the main benefit of nest reuse by Vermilion Flycatchers is enhanced nest success.

ACKNOWLEDGMENTS

I thank the residents of Ft. Clark Springs for allowing this research in their community. I also thank T. A. Galloway for laboratory space and insect identification, P. S. Warren and E. D. Klepper for assistance with site logistics, and M. D. Boyd, S. J. A. Coles, N. L. Marino, H. R. McGaha, and Patricia Sullivan for field assistance. Funds for this research were provided by a graduate fellowship and the George A. Lubinsky Memorial Scholarship from the University of Manitoba, Frank M. Chapman Memorial Awards, and a Discovery Grant from the Natural Sciences and Engineering Research Council to S. G. Sealy.

LITERATURE CITED

Allaire, P. N. 1972. Field Sparrow uses abandoned nest for August brood. Auk 89:886.

Bancroft, G. T. 1987. Mating system and nesting phenology of the Boat-tailed Grackle in central Florida. Florida Field Naturalist 15:1–18.

Barclay, R. M. R. 1988. Variation in the costs, benefits, and frequency of nest reuse by Barn Swallows (*Hirundo rustica*). Auk 105:53–60.

Bent, A. C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U.S. National Museum Bulletin Number 197.

Biedenneg, D. W. 1983. Time and energy budgets of the Mockingbird (*Mimus polyglottos*) during the breeding season. Auk 100:149–160.

Bowen, R. V. 1997. Townsend's Solitaire (*Myadestes townsendi*). The birds of North America. Number 269.

Briskie, J. V. and S. G. Sealy. 1988. Nest re-use and egg burial in the Least Flycatcher, *Empidonax minimus*. Canadian Field-Naturalist 102:729–731.

Brown, C. and M. B. Brown. 1996. The evolution of coloniality and Cliff Swallows. University of Chicago Press, Chicago, Illinois, USA.

Brown, J. M. 1994. Mexican Jay (*Aphelocoma ultramarina*). The birds of North America. Number 118.

Carothers, S. W. 1974. Breeding ecology and time-energy budget of male Vermilion Flycatchers and comments on the social organization of southwestern riparian birds. Dissertation. University of Illinois, Chicago, USA.

Cavitt, J. F., A. T. Pearse, and T. A. Miller. 1999. Brown Thrasher nest reuse: a time saving resource, protection from search-strategy predators, or cues for nest-site selection? Condor 101:859–862.

Clark, L. and J. R. Mason. 1985. Use of nest material as insecticidal and antipathogenic agents by the European Starling. Oecologia 67:169–176.

Conrad, K. F. and R. J. Robertson. 1993. Clutch size in Eastern Phoebes (*Sayornis phoebe*). I. The cost of nest building. Canadian Journal of Zoology 71: 1003–1007.

Curson, D., C. B. Goguen, and N. E. Mathews. 1996. Nest site re-use in Western Wood Pewees. Wilson Bulletin 108:378–379.

Farquhar, C. C. and K. L. Ritchie. 2002. Black-tailed Gnatcatcher (*Polioptila melanura*). The birds of North America. Number 690.

Flood, N. J. 2002. Scott's Oriole (*Icterus parisorum*). The birds of North America. Number 608.

Fretwell, S. D. and H. L. Lucas Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:16–36.

Friesen, L. E., V. E. Wyatt, and M. D. Cadman. 1999. Nest reuse by Wood Thrushes and Rose-breasted Grosbeaks. Wilson Bulletin 111:132–133.

Gillihan, S. W. and B. Byers. 2001. Evening Grosbeak (*Coccothraustes verspertinus*). The birds of North America. Number 599.

Gilman, M. F. 1909. Among the thrashers in Arizona. Condor 11:49–54.

Gilman, M. F. 1915. A forty-acre bird census at Sacaton, Arizona. Condor 17:86–90.

Greenlaw, J. S. 1996. Spotted Towhee (*Pipilo maculatus*). The birds of North America. Number 263.

Harms, K. E., L. D. Beletsky, and G. H. Orians. 1991. Conspecific nest parasitism in three species of New World blackbirds. Condor 93:967–974.

Hensler, G. L. and J. D. Nichols. 1981. The Mayfield

method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42–53.

Hill, G. E. 1993. House Finch (*Carpodacus mexicanus*). The birds of North America. Number 46.

Hines, J. E. and J. R. Sauer. 1989. Program CONTRAST. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. http://www.mbrpwrc.usgs.gov/software.html (accessed 1 February 2005).

International Bird Census Committee (IBCC). 1970. Recommendations for an international standard for a mapping method in bird census work. Swedish Natural Resources Council, Stockholm. Bulletin of Ecological Research Committee 9:49–52.

Kren, J. and A. C. Zoerb. 1997. Northern Wheatear (*Oenanthe oenanthe*). The birds of North America. Number 316.

Kunzmann, M. R., K. Ellison, K. L. Purcell, R. R. Johnson, and L. T. Haight. 2002. California Towhee (*Pipilo crissalis*). The birds of North America. Number 632.

Lindell, C. 1996. Patterns of nest usurpation: when should species converge on nest niches? Condor 98:464–473.

Lowther, P. E., S. M. Lanyon, and C. W. Thompson. 1999. Painted Bunting (*Passerina ciris*). The birds of North America. Number 398.

Mason, P. 1985. The nesting biology of some passerines of Buenos-Aires, Argentina. Ornithological Monographs 36:954–972.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

McNair, D. B. 1984. Reuse of other species' nests by Lark Sparrows. Southwestern Naturalist 29:506–509.

McNair, D. B. 1985. A comparison of oology and nest record card data in evaluating the reproductive biology of Lark Sparrows, *Chondestes grammacus*. Southwestern Naturalist 30:213–224.

Møller, A. P. 1994. The Barn Swallow and sexual selection. Oxford University Press, Oxford, United Kingdom.

Møller, A. P. and J. Erritzøe. 1996. Parasite virulence and host immune defense: host immune response is related to nest reuse in birds. Evolution 50:2066–2072.

Mountjoy, D. J. and R. J. Robertson. 1988. Nest construction tactics in the Cedar Waxwing. Wilson Bulletin 100:128–130.

Nice, M. M. 1937. Studies of the life history of the Song Sparrow. Volume 1. Transactions of the Linnaean Society. New York, USA.

Nicholson, C. P. 1981. Likely nest reuse by a Field Sparrow. Journal of Field Ornithology 52:235.

Nolan Jr., V., E. D. Ketterson, D. A. Crista, C. M. Rogers, E. D. Clotfelter, R. C. Titus, S. J. Schoech, and E. Snajdr. 2002. Dark-eyed Junco (*Junco hyemalis*). The birds of North America. Number 716.

Peer, B. D. and S. G. Sealy. 2000. Conspecific brood parasitism and egg rejection in Great-tailed Grackles. Journal of Avian Biology 31:271–277.

Sheppard, J. M. 1996. Le Conte's Thrasher (*Toxostoma lecontei*). The birds of North America. Number 230.

Stahle, D. W. and M. K. Cleavland. 1988. Texas drought history reconstructed and analyzed from 1698 to 1980. Journal of Climate 1:59–74.

Stanback, M. T. and A. F. Dervan. 2001. Within-season nest site fidelity in Eastern Bluebirds: disentangling the effects of nest success and parasite avoidance. Auk 118:743–745.

Styrsky, J. N. 2005. Influence of predation on nest-site reuse by an open-cup nesting neotropical passerine. Condor 107:133–137.

Taylor, W. K. and H. Hanson. 1970. Observations on the breeding biology of the Vermilion Flycatcher in Arizona. Condor 82:315–319.

van Riper III, C. 1976. Aspects of House Finch breeding biology in Hawaii. Condor 78:224–229.

Weathers, W. W. 1992. Scaling nestling energy requirements. Ibis 134:142–153.

Weathers, W. W. 2001. Erratum. Ibis 143:708.

Whitehead, D. R. and T. Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*). The birds of North America. Number 614.

Wolf, B. O. and S. L. Jones. 2000. Vermilion Flycatcher (*Pyrocephalus rubinus*). The birds of North America. Number 484.

Yard, H. K. and B. T. Brown. 1999. Willow Flycatcher nest reuse in Arizona. Journal of Field Ornithology 70:211–213.

Yeh, P. J., M. E. Hauber, and T. D. Price. 2007. Alternative nesting behaviors following colonization of a novel environment by a passerine bird. Oikos 116:1473–1480.

The Wilson Journal of Ornithology 120(2):345–352, 2008

NATURAL HISTORY AND BREEDING BIOLOGY OF THE RUSTY-BREASTED ANTPITTA (*GRALLARICULA FERRUGINEIPECTUS*)

ALINA M. NIKLISON,[1,5] JUAN I. ARETA,[1,2,3] ROMAN A. RUGGERA,[1] KARIE L. DECKER,[1] CARLOS BOSQUE,[4] AND THOMAS E. MARTIN[1]

ABSTRACT.—We provide substantial new information on the breeding biology of the Rusty-breasted Antpitta (*Grallaricula ferrugineipectus ferrugineipectus*) from 40 nests during four consecutive breeding seasons at Yacambú National Park in Venezuela. Vocalizations are quite variable in *G. ferrugineipectus*. Nesting activity peaked in April when laying began for half of all nests monitored. The date of nest initiation pattern suggests this species is single-brooded. Both parents incubate and the percent of time they incubate is high (87–99%) throughout the incubation period. The incubation period averaged (± SE) 17.0 ± 0.12 days, while the nestling period averaged 13.37 ± 0.37 days. *G. f. ferrugineipectus* has the shortest developmental time described for its genus. Time spent brooding nestlings decreased as nestlings grew, but was still greater at pin feather break day than observed in north temperate species. The growth rate constant based on mass (k = 0.41) and tarsus length (k = 0.24) was lower than the k for north temperate species of similar adult mass. All nesting mortality was caused by predation and overall daily survival rate (± SE) was relatively low (0.94 ± 0.01) yielding an estimated 15% nest success. *Received 13 January 2007. Accepted 25 July 2007.*

Breeding biology and life history traits of most neotropical birds are poorly known and antpittas are no exception (Krabbe and Schulenberg 2003, Rice 2005). The small antpitta genus *Grallaricula* comprises eight species (Krabbe and Schulenberg 2003). Nest descriptions and scanty breeding information are available for *G. ferrugineipectus*, *G. nana*, *G. flavirostris*, and *G. peruviana* (Krabbe and Schulenberg 2003). The most detailed study to date is that by Schwartz (1957) for the Rusty-breasted Antpitta (*G. f. ferrugineipectus*) where the description of nest and breeding biology was based on only three nests in a forest (850–900 m elevation) south of Petare, Edo. Miranda, Venezuela. Information on the exact length of incubation and nestling stages, parental behavior, predation rates, and nestling growth rates remain unknown. Our objective is to provide data on these previously undocumented life history traits and other natural history information for *G. f. ferrugineipectus* based on detailed field observations. Field work was conducted during four consecutive breeding seasons from 2003 to 2006 at Yacambú National Park, Edo. Lara, a montane cloud forest area in north-central Venezuela (09° 42′ N, 69° 42′ W; 500–2,200 m elevation). Means are presented with one standard error (SE) unless otherwise noted.

OBSERVATIONS

Distribution and Habitat.—The Rusty-breasted Antpitta has a disjunct distribution ranging from Venezuela and northern Colombia (subspecies *ferrugineipectus* and *rara*) to northern Peru and western Bolivia (subspecies *leymebambae*) (Ridgely and Tudor 1994, Krabbe and Schulenberg 2003). *G. f. ferrugineipectus* in Venezuela has a wide altitudinal distribution, ranging from 250 to 2,200 m (Giner and Bosque 1998) and inhabits tropical and subtropical areas of the Andes of Mérida and western Lara, Falcón, Yaracuy, Distrito Federal, and Miranda (De Schauensee and Phelps 1978). We worked on this species in Yacambú from its upper distributional limit at 1,600 m elevation down to 1,300 m. We found it mostly in secondary growth wet forest with a closed upper story (7–15 m) and an under-

[1] USGS, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA.

[2] CICyTTP-CONICET, Materi y España, Diamante (3105), Entre Ríos, Argentina.

[3] Grupo FALCO, Calle 117 Nro 1725 e/66 y 67, La Plata (1900), Argentina.

[4] Departamento de Biología de Organismos, Universidad Simón Bolívar, Apdo. 89000, Caracas 1080-A, Venezuela.

[5] Corresponding author; e-mail: alinanik@yahoo.com

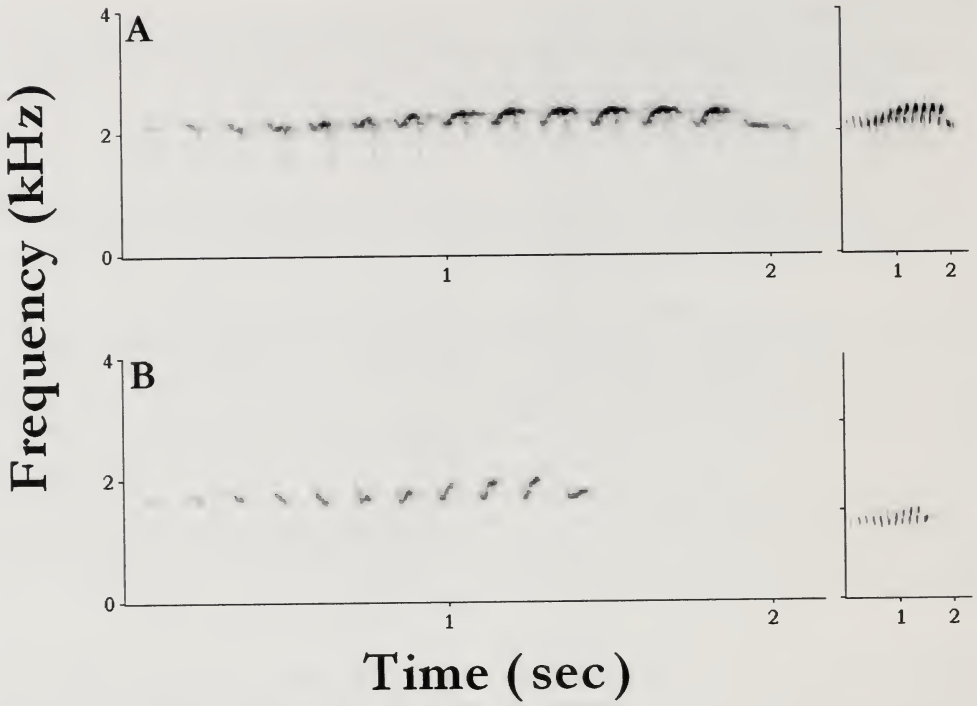


FIG. 1. Vocalization spectrograms of *G. f. ferrugineipectus*. (A) Adult main song (probably male), recorded by J. I. Areta, 13 June 2006. (B) Voice on the nest (unknown gender) from a videotape by L. A. Biancucci, 22 April 2005. Both recordings were during the breeding season at Yacambú National Park, Lara, Venezuela. Spectrograms on the right are reduced in scale to show overall pattern.

growth occupied mostly by vine tangles, small tree saplings, and *Chamaedorea* spp. palms.

Foraging.—Individual Rusty-breasted Antpittas were consistently observed foraging between 0.5 and 2.0 m above ground, but not hopping on the ground like many *Grallaria* spp. (Stiles 1992; A. M. Niklison, pers. obs.). We did not quantify foraging behavior, but most foraging involved hopping along branches, peering at leaves, and sallying to gather flying insects. Schwartz (1957) also reports birds descending from perches to the ground to catch insects and immediately flying back to the perch. Additionally, we had a single observation of a curious foraging behavior where a bird perched on a small branch and vigorously shook it with both feet to flush insects which were then caught by sallying.

Vocalizations.—The Rusty-breasted Antpitta was vocal throughout the day during the breeding season. Singing activity peaked in the early morning and late afternoon. Adults (presumably only males sing, Schwartz 1957) were recorded singing under natural conditions and after playback with their own voice. The loudsong of *G. f. ferrugineipectus* consisted of a series of 14–17 plaintive and whistled chevron shaped notes (on the sonogram) that increase slowly in pitch, and then descend at a faster rate and ending in one or two distinctive lower pitched and flatter notes (Fig. 1A). The unsolicited loudsong lasted 2 sec and ranged from 1.2 to 2.6 kHz with a high frequency harmonic documented at 14 kHz in some individuals. The large variation in timing and rate of pitch increase prompted Schwartz (1957) to distinguish two loudsongs, and our recordings (n = 8) concurred. The loudsongs seem to grade into each other through many intermediates spanning the two extremes (Schwartz 1957 provides a phonetic notation of the voices), and they might be better understood as extremes within a single extremely variable loudsong. Spontaneous vocalizations usually consisted of 14 notes and remained constant after playback or when ex-

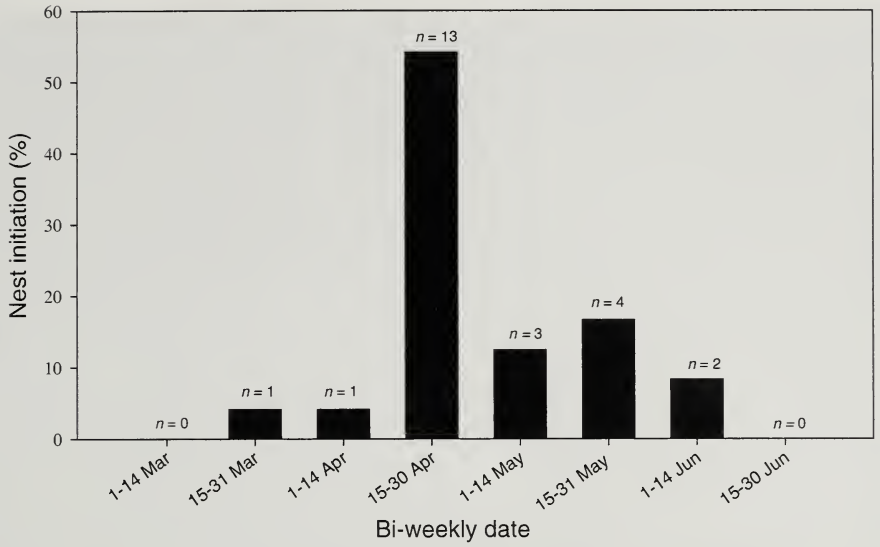


FIG. 2. Percent of nests that were initiated (first egg laid) by date for *G. f. ferrugineipectus* at Yacambú National Park, Lara, Venezuela, March to July, 2003–2006. Only nests for which initiation date was observed are included (n = 24).

cited, unlike *G. lineifrons* in which the number of notes decreased from 21 in unsolicited vocalization to 13–15 notes after playback (Robbins et al. 1994). The loudsong of the nominal subspecies at Yacambú differs strikingly from that of the allopatric *G. f. leymebambae* whose loudsong is a monotonous series of whistles (Mayer 2000, Krabbe and Schulenberg 2003). The loudsong of *G. f. ferrugineipectus* recalls that of *G. nana* and *G. lineifrons* in basic pattern, note shape, and frequency range differing most notably in pitch, speed, and length (Robbins et al. 1994; J. I. Areta, pers. obs.).

We recorded a previously unreported shorter, softer, and relatively unstructured and variable song emitted by a bird on the nest during the 2 min that preceded leaving the nest for an off-bout (Fig. 1B). This bird was not immediately replaced by any other and we suspect this might be a contact call eliciting parental switch. A similar soft voice was uttered in a parental switch during incubation in more than one occasion (video recording data). Schwartz (1957) also describes a short single-note call, but we did not hear or record this call at our study site.

Nesting Chronology.—The nesting period for this species was thought to start in mid May and limited to the earliest part of the rainy season (Schwartz 1957). However, in Yacambú the rainy season spans from mid-April until mid-July. We worked at this site from the beginning of March until early July each year and found that nest building and egg laying started several weeks before the rainy season and continued through June. The peak in nesting activity occurred at the beginning of the rainy season in the last 2 weeks of April when 54% of nests were initiated (Fig. 2). We found 40 nests between March and July for all years combined. The earliest active nest was found empty on 27 March 2006 and had two eggs by 31 March 2006. The latest date of nest initiation was 7 June 2006.

On two occasions, nest building activity was observed within 3 days of predation events and within 10 m of the depredated nests. Given the proximity and timing, we assume these reflect re-nesting attempts, but the pattern of initiation observed (Fig. 2) suggests this species is single-brooded; pairs that successfully fledged young were not observed initiating a new nest in the same season.

Clutch Size and Eggs.—All nests that were occupied (n = 37) had two eggs or nestlings similar to that reported by Schwartz (1957). Clutch size in *Grallaricula* varies between one in *G. nana* and *G. peruviana*, and two in *G. ferrugineipectus*, and between one and two

FIG. 3. Top view of the nest and egg of *G. f. ferrugineipectus*, Yacambú National Park. Photograph by A. M. Niklison, 19 April 2005.

in *G. flavirostris* (Holley et al. 2001; Greeney et al. 2004a, 2004b; Greeney and Sornoza 2005).

Eggs were short, sub-elliptical to oval in shape, and usually pale greenish or grayish with variously shaped markings in brown shades over the entire surface. The greenish background color of *G. f. ferrugineipectus* eggs (Fig. 3) is different from the pale coffee-brown with darker brown blotches described for *G. nana* (Greeney and Sornoza 2005), *G. cucullata* (Schonwetter 1967), *G. flavirostris* (Holley et al. 2001), and *G. peruviana* (Greeney et al. 2004a, 2004b). Two clutches had eggs with brownish background color. The pattern of markings closely resembles that of *G. nana* (Fig. 3; and Fig. 1 in Greeney and Sornoza 2005).

We weighed 15 eggs at eight nests between day zero and day 2 of the incubation period using an ACCULAB portable electronic scale (precision 0.001 g). Individual eggs varied from 2.40 to 3.02 g among the eight nests and averaged 2.78 ± 0.05 g, which was ~17% of average adult weight (16.48 ± 0.43 g, n = 10). Egg dimensions averaged 1.88 ± 0.13 cm in length and 1.73 ± 0.15 cm in width (Mitutoyo digital caliper, precision 0.01 mm, n = 3). Volume was estimated using Hoyt's (1979) formula (0.51 × length × [width^2]) and averaged 2.84 ± 0.29 cm^3.

Nests and Nest Placement.—Nests were unstable and difficult to remove without destroying them, as is common for *G. f. ferrugineipectus* and other *Grallaricula* (Greeney et al. 2004b, Greeney and Sornoza 2005). Nests were in secondary growth areas in microhabitats with abundant vine tangles. Construction was simple consisting of a slightly concave twig platform on top of which black rootlets were knitted in a shallow cup finished with thin and brown rootlets without moss. They were usually supported by slender vines or placed on top of a palm leaf from 0.5 to 2.0 m in height, averaging 1.30 ± 0.14 m high (n = 17). Unlike *G. peruviana* (Greeney et al. 2004b), only one adult participated in nest construction.

We measured size of nests for outer diameter (from edge to edge), inner diameter (cup), outer height (exterior bottom-to-top), and inner height (bottom-to-top of cup) of 20 nests

(Fig. 3). Inner diameter averaged 6.0 ± 0.16 cm, outer diameter 10.5 ± 0.30 cm, inner height 2.2 ± 0.15 cm, and outer height 4.36 ± 0.31 cm. Nest shape, size, building materials, and poor support are much like those of *G. nana* (Fig. 1 in Greeney and Sornoza 2005), but differ from *G. flavirostris* and *G. peruviana* which attach their mossy nests to branches (Holley et al. 2001; Greeney et al. 2004a, 2004b).

Incubation Period and Behavior.—We measured duration of incubation periods, when possible, as the number of days between the last egg laid and the last egg hatched (Briskie and Sealy 1990, Martin 2002). Eggs hatched synchronously in all cases, suggesting that incubation began when the last egg was laid contradicting Schwartz's (1957) suggestion that incubation began with the first egg. The incubation period varied from 16 to 17.5 days and averaged 17.0 ± 0.12 days (n = 4) (also see Schwartz 1957). *G. f. ferrugineipectus* has the shortest incubation period described for the genus; *G. flavirostris* has an incubation period of 17–21 days (Holley et al. 2001) and *G. peruviana* has an incubation period of 20 days (Greeney et al. 2004b).

We measured parental nest attentiveness (percent time on the nest incubating) and duration of incubation bouts by videotaping nests for 6 to 8 hrs starting within 30 min of sunrise (Martin and Ghalambor 1999, Martin 2002). Both adults share incubation and they exchange bouts on the nest. Nest attentiveness increased mildly (r = 0.47, P = 0.06, df = 16) from day 2 to day 17 of incubation, averaging 94.6 ± 1.4% overall. However, the increase was due to two nests on day 2 in which both parents stayed off the nest for a long period in the afternoon and caused lower nest attentiveness estimates (82.3 ± 0.75%). Variability in attentiveness in the first few days of incubation is common in tropical birds (T. E. Martin, unpubl. data). If these two nests are excluded, nest attentiveness did not change from day 2 to day 17 of the incubation period (r = 0.20, P = 0.47, df = 14) and averaged 96.3 ± 0.95%. On and off-bout durations were unrelated to incubation age (both $r <$ 0.3, $P >$ 0.05). On bouts averaged 66.53 ± 4.44 min, n = 17. Nests were nearly continuously occupied.

A general comparison of nest attentiveness and on-bout/off-bout duration among species of *Grallaricula* is not possible due to the lack of published data. However, information for *G. nana* indicates lower incubation attentiveness (65%, Greeney and Sornoza 2005), shorter on-bouts averaging (± SD) 53.8 ± 44.3 min, and longer off-bouts averaging (± SD) 10.6 ± 15.7 min than for *G. f. ferrugineipectus*. The incubation day of these measurements was not reported and we cannot provide a more precise comparison.

Adults during incubation performed nest maintenance by arranging edge sticks or inner cup rootlets and by bringing material to the nest when switching, as also observed by Schwartz (1957). Adults frequently rotated their bodies and stood to examine and possibly rotate the eggs, as also observed in *G. nana* (Greeney and Sornoza 2005).

Nestling Period and Brooding Behavior.—We measured the nestling period as the number of days from hatching to fledging. The nestling period varied from 12 to 14 days and averaged 13.37 ± 0.37 days (n = 4) similar to the 13-day period reported by Schwartz (1957) but relatively shorter than the reported 14–16 days for *G. flavirostris* (Holley et al. 2001).

Nestlings are naked at hatching and the gape is deep orange. The juvenile plumage is a thick wooly down that is hair-like rather than feather-like. The plumage tract of the head during development is reduced to a single narrow track that resembles a scalp-lock.

Adults provisioned young an average of 3.77 trips/hr (n = 1) on the first day of the nestling period, 3.91 ± 1.06 (n = 3) on day 2, 4.48 ± 0.07 (n = 2) on day 6, and on day 8 (day the pin feather of primary 8 breaks its sheath) they fed 9.08 times/hr (n = 1). Both parents brought spiders, butterflies, crickets, cockroaches, larvae, and beetles as feeding items (this study; Schwartz 1957).

The percent of time spent brooding during the nestling period was averaged across bouts for each nest and then averaged across nests, with the SE reflecting this cross-nest mean. Brooding time averaged 98% (n = 24 bouts, 1 nest) on day 1, 84 ± 3% (n = 68, 3 nests) on day 2, 90 ± 3% (n = 52, 2 nests) on day 6, and 61% (n = 9, 1 nest) on day 8, pin-break day. Time spent brooding is higher ($P <$ 0.001) than published for some north-tem-

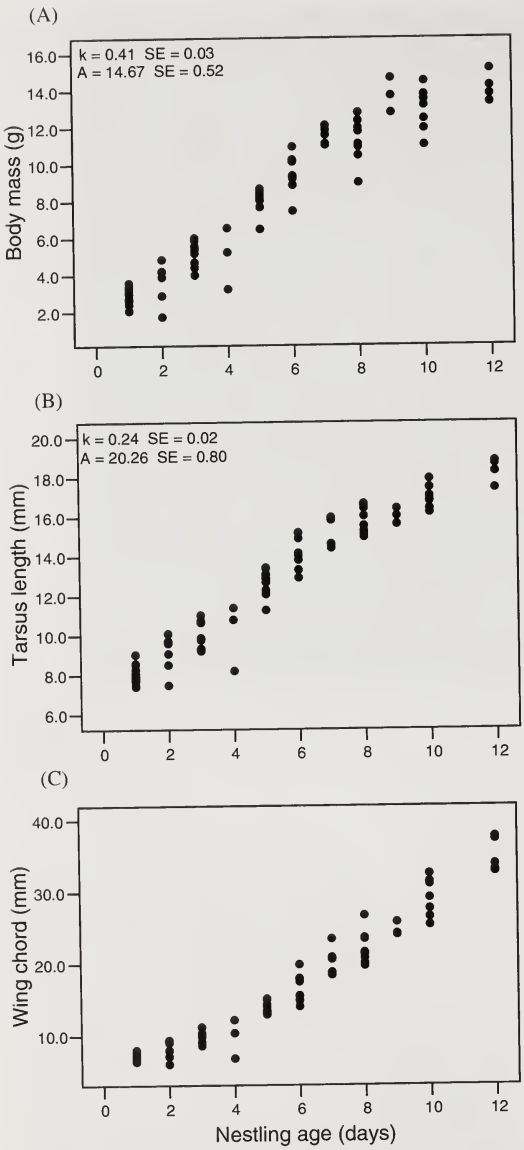


FIG. 4. Nestling measurements of *G. f. ferrugineipectus* at Yacambú National Park plotted against age: (A) Mass, (B) Tarsus length, and (C) Wing-chord. Growth rate constant (k) and asymptote (A) are indicated for mass and tarsus.

perate birds; for example the Song Thrush (*Turdus philomelos*) broods only 29% of the time on the day that pin feathers break their sheaths (Hill et al. 1999).

Nestling Growth.—We measured nestling tarsus length and wing chord (Mitutoyo digital calipers, 0.01 mm precision) and weighed nestlings (ACCULAB digital electronic scales, 0.001 g precision). We estimated growth rate using the formula $W(t) = A/\{1 + e^{[-K(t-t_i)]}\}$, where $W(t)$ refers to mass or tarsus length at day t, k is the growth rate constant, A is the estimated asymptotic mass or tarsus length, and t_i is the inflection point of change from accelerating to decelerating growth, following Ricklefs (1967). The growth rate constant for mass (Fig. 4) was lower than the k for unrelated north temperate passerine species that averaged $k = 0.52 \pm 0.05$ ($n = 4$) for a similar adult weight (16.2–17.5 g) based on data in Remeš and Martin (2002). Nestlings (10–13 days of age) did not "play dead" during measurements in contrast to Schwartz (1957). Nestling weight on day 12, the day before normal fledging averaged 14.09 ± 0.39 g ($n = 4$) which was 85% of adult body mass. The Rusty-breasted Antpitta fledged with a larger relative body mass ($t_3 = 3.81$, $P = 0.032$) than similar-sized but unrelated north temperate species 75 ± 5%, $n = 4$ (Remeš and Martin 2002). This may reflect the longer ($t_3 = 10.33$, $P = 0.002$) time spent in the nest compared with north temperate species.

Nest Predation and Success.—We did not find all nests during nest-building; 16 nests were found during nest-building, 19 during incubation, and 5 during the nestling stage. Consequently, we calculated daily survival rates using the Mayfield method (Mayfield 1975, Hensler and Nichols 1981). Three nests were abandoned during building and one was lost due to investigator disturbance; these were excluded from the Mayfield estimates. Twenty-five of the remaining 36 nests were lost to predation and the rest were successful. One nest was depredated during the laying period, 18 during incubation, and 6 during the nestling period. Overall daily survival rate was 0.94 ± 0.012 ($n = 409.5$ exposure days, 36 nests). Daily survival rates were 0.931 ± 0.067 for the laying period, 0.929 ± 0.016 for the incubation period, and 0.958 ± 0.017 for the nestling period. Only 15% of *G. f. ferrugineipectus* nests were successful as estimated by the Mayfield method. North temperate passerine species have a higher estimated nesting success ($t_{17} = 6.876$, $P < 0.001$), averaging 42.43 ± 0.040% ($n = 18$) (Martin 1992).

DISCUSSION

Our data are typical for many tropical species, where they exhibit a slower pace of life

compared with north temperate species, including small clutch size, slow development during both incubation and nestling stages despite high parental care, and lower nesting success (Martin 1996, Martin et al. 2000, Martin 2002, Martin et al. 2007). Contrary to views that these traits might reflect long breeding seasons (reviewed by Martin 1996), the breeding season was similar in length to north temperate systems, and the species did not appear to be multi-brooded suggesting that alternative explanations need to be sought. The behavior of sharing incubation duties by both males and females is relatively uncommon in north temperate passerines but common in a number of endemic tropical groups (Martin et al. 2007). The high brooding attentiveness late into the nestling stage may also be common in tropical endemics, but these behaviors have been neglected and deserve further attention.

ACKNOWLEDGMENTS

We thank M. J. Foguet, L. A. Biancucci, Alison Cox, W. A. Cox, J. R. Lang, Andrew Hoar, A. A. Majewska, and William Goulding for valuable help in the field. We are also grateful to Muttulingam Sanjayan, J. L. Hierro, R. J. Fletcher Jr., and two anonymous reviewers for helpful comments on this manuscript. This study was supported by NSF grants DEB-9981527 and DEB-0543178 to T. E. Martin. Permit numbers are DM/0000237 from FONACIT; PA-INP-005-2004 from INPARQUES; and 01-03-03-1147 from Ministerio del Ambiente.

LITERATURE CITED

Briskie, J. and S. G. Sealy. 1990. Evolution of short incubation periods in the parasitic cowbirds, *Molothrus* spp. Auk 107:789–793.

De Schauensee, R. M. and W. H. Phelps. 1978. A guide to the birds of Venezuela. Princeton University Press, Princeton, New Jersey, USA.

Giner, S. and C. Bosque. 1998. Distribución altitudinal de las subfamilias Grallarinae, Formicariinae y Thamnophilinae (*Aves*, *Formicariidae*) en Venezuela. Boletin de la Sociedad Biologica de Chile 69:115–121.

Greeney, H. F. and F. Sornoza. 2005. The nest and egg of the Slate-crowned Antpitta (*Grallaricula nana*) with observations on incubation behavior in southern Ecuador. Ornitologia Neotropical 16: 137–140.

Greeney, H. F., E. C. Hannelly, and M. Lysinger. 2004a. First description of the nest and vocalizations of the Peruvian Antpitta (*Grallaricula peruviana*) with a northward range extension. Cotinga 21:14–17.

Greeney, H. F., R. A. Gelis, E. C. Hannelly, and P. J. DeVries. 2004b. The egg and incubation period of the Peruvian Antpitta (*Grallaricula peruviana*). Ornitologia Neotropical 15:403–406.

Hensler, G. L. and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42–53.

Hill, I. F., B. Cresswell, and R. E. Kenward. 1999. Comparison of brooding patterns between Blackbird (*Turdus merula*) and Song Thrush (*Turdus philomelos*). Bird Study 46:122–126.

Holley, D. R., C. A. Lindell, M. A. Roberts, and L. A. Biancucci. 2001. First description of the nest, nest site, and eggs of the Ochre-breasted Antpitta. Wilson Bulletin 113:435–438.

Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73–77.

Krabbe, N. and T. S. Schulenberg. 2003. Family *Formicariidae* (ground-antbirds). Pages 682–731 *in* Handbook of the birds of the world. Volume 8. Broadbills to tapaculos (J. del Hoyo, A. Elliot, and D. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 *in* Ecology and conservation of neotropical migrants (J. M. Hagan and D. W. Johnston, Editors). Smithsonian Institution Press, Washington D.C., USA.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? Journal of Avian Biology 27:263–272.

Martin, T. E. 2002. A new view for avian life history evolution tested on an incubation paradox. Proceedings of the Royal Society of London, Series B 269:309–316.

Martin, T. E. and C. K. Ghalambor. 1999. Males helping females during incubation. Required by microclimate or constrained by nest predation? American Naturalist 153:131–139.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. Science 287:1482–1485.

Martin, T. E., S. K. Auer, R. D. Bassar, A. M. Niklison, and P. Lloyd. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. Evolution 61: 2558–2569.

Mayer, S. 2000. Birds of Bolivia 2.0. Bird Songs International, Enschede, The Netherlands.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Remeš, V. and T. E. Martin. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56:2505–2518.

Rice, N. H. 2005. Phylogenetic relationships of ant-

pitta genera. (Passeriformes: Formicariidae). Auk 122:673–683.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978–983.

Ridgely, R. S. and G. Tudor. 1994. Birds of South America. Volume 2. University of Texas Press, Austin, USA.

Robbins, M. B., N. Krabbe, G. H. Rosenberg, R. S. Ridgely, and F. Sornoza M. 1994. Notes on the natural history of the Crescent-faced Antpitta. Wilson Bulletin 106:169–173.

Stiles, F. G. 1992. A new species of antpitta (Formicariidae: *Grallaria*) from the eastern Andes of Colombia. Wilson Bulletin, 104:389–399.

Schonwetter, M. 1967. Handbuch der Oologie. Akademie-Verlag, Berlin, Germany.

Schwartz, P. 1957. Observaciones sobre *Grallaricula ferrugineipectus*. Boletin de la Sociedad Venezolana de Ciencias Naturales 18:42–62.

The Wilson Journal of Ornithology 120(2):353–365, 2008

FORAGING ECOLOGY OF PARROTS IN A MODIFIED LANDSCAPE: SEASONAL TRENDS AND INTRODUCED SPECIES

GREG D. MATUZAK,[1,4] M. BERNADETTE BEZY,[2] AND DONALD J. BRIGHTSMITH[3]

ABSTRACT.—We studied the diet and foraging ecology of a community of six psittacines in western Costa Rica. All had a varied diet with clear seasonal changes in preferred food items, mostly due to changes in plant phenology. There was a significant relationship between parrot mass and food types: larger-bodied parrots consumed more seeds and smaller-bodied parakeets consumed more fruit pulp. Leaves, bark, and lichen were also consumed by most psittacines. Most parrots consumed more plant species in the dry season when food availability was at its peak. Levins' niche breath showed varying levels of diet specialization among species and, for some species, variation among seasons. There was less similarity in seasonal psittacine diets when compared to overall diets. Scarlet Macaws (*Ara macao*) under study were captive raised and released which may have contributed to their narrow diet breadth as they may have lacked the knowledge or experience to exploit additional food sources. Non-native and cultivated species comprised 76% of the diet of Scarlet Macaws, and averaged 28% for all other species. This suggests that foraging parrots may have increased conflicts with humans as landscapes become increasingly modified. Forest restoration strategies should augment the abundance of food species consumed when overall food supply is at its annual low. *Received 20 February 2007. Accepted 4 September 2007.*

Knowledge about diets is fundamental for understanding species' niches, roles in communities, and potential impacts on other species (Moegenburg and Levey 2003, French and Smith 2005, Munshi-South and Wilkinson 2006). Knowledge of diet is also needed to design effective conservation and management strategies, and to predict how landscape level changes may affect species (Pitter and Christiansen 1995, Bennett and Owens 1997). Approximately one third of all psittacines are threatened with extinction and with anthropogenic changes, many species have become locally or regionally extinct (Collar 1997). However, in some cases parrot species increase in abundance with landscape conversion and become agricultural pests (Forshaw 1989, Bucher 1992). Overall, the natural history of psittacines is poorly known with little or no information on the diet of over 75% of the recognized species (Collar 1998). This lack of basic diet information poses problems for those who work to understand and conserve threatened parrots, mitigate agriculture damage, and understand the impacts of parrots on vegetative communities (Collar 1998, Moegenburg and Levey 2003).

Parrots feed predominantly on seeds, fruit pulp, and flowers along with variable amounts of leaves, bark, nectar, and insects (Forshaw 1989, Sazima 1989, Pizo et al. 1995). Parrots eat ripe and unripe fruits, and many species consume large amounts of immature and mature seeds, making some psittacines effective pre-dispersal seed predators (Desenne 1994, Pizo et al. 1995). Pollination and seed dispersal have rarely been recorded for parrots (Fleming et al. 1985, Cotton 2001) with most parrot feeding leading to some reduction in plant fitness (Galetti 1993, Ragus-Netto 2005). Identifying and conserving key food resources and their habitats may be vital to the long term conservation of some parrot communities.

We conducted a 2-year study on the foraging ecology and diet of a community of six sympatric parrot species in western Costa Rica. Our objectives were to document: (1) the plant species and plant parts consumed by each parrot species, (2) the level of seed predation and frugivory for each species, (3) seasonal diet changes, and (4) key resources used by each psittacine species. We also discuss the importance of introduced and cultivated plant

[1] 10090 Skyline Drive, Grass Valley, CA 95945, USA.

[2] University of Costa Rica, Department of Biology, San Jose, Costa Rica.

[3] Schubot Exotic Bird Health Center, Department of Veterinary Pathobiology, Texas A&M University, College Station, TX 77843, USA.

[4] Corresponding author;
e-mail: gmatuzak@hotmail.com

species to foraging parrots in view of the changing landscape throughout the Neotropics.

METHODS

Study Area.—This study was conducted on the southern Nicoya Peninsula in the Province of Puntarenas, western Costa Rica. The primary research site was Curú Wildlife Refuge (09° 47′ N, 84° 56′ W). Curú is a private wildlife refuge and working farm of 1,492 ha with 70% forested habitats, and 30% pastures and plantations (Schutt and Vaughan 1995). Curú is part of the Peninsular Biological Corridor, a loosely connected network of small forested fragments on the southern Nicoya Peninsula (Vaughan et al. 1994). We collected additional data on Tortugas and Negritos islands, ~2 and 5 km, respectively, from Curú in the Nicoya Gulf.

Rainfall totals ~200 cm per annum and is strongly seasonal with a wet season from May to November, and a dry season from December to April (months with <10 cm of precipitation). The average temperature throughout the year is 27.3° C (Vaughan et al. 1994). The site is at the boundary of tropical dry forest, tropical moist forest, and tropical premontane life zones (Tosi 1969), and contains a mosaic of mangroves (*Avicennia*, *Rhizophora*, *Laguncularia*), dry deciduous forest, semi-deciduous forests, mixed coconut (*Cocos*) forest, beaches, evergreen forest, pastures, and plantations of *Tectona grandis* and *Mangifera indica* (Vaughan et al. 1994).

Six psittacine species occur on southern Nicoya Peninsula: Scarlet Macaw (*Ara macao*—900 g), Yellow-naped Amazon (*Amazona auropalliata*—480 g), Red-lored Amazon (*A. autumnalis*—420 g), White-fronted Amazon (*A. albifrons*—230 g), Orange-fronted Parakeet (*Aratinga canicularis*—80 g), and Orange-chinned Parakeet (*Brotogeris jugularis*—65 g) (weights from Stiles and Skutch 1989). Scarlet Macaw is considered an endangered species (Appendix 1 of the Convention on International Trade in Endangered Species [CITES]). The small population of macaws in the project area was established in an area absent of a wild population in 1999 through a reintroduction program. Macaws observed were a group of 9–12 birds that had been released 4 years prior to the onset of our study (Brightsmith et al. 2005). Yellow-naped Parrot is a threatened species (CITES 2002) and the area contains one of the largest known roosting populations of the species in Costa Rica with a minimum of 300 individuals (Matuzak and Brightsmith 2007).

Parrot Foraging Observations.—We established six transects in areas known to be frequented by parrots to document psittacine diets. Transects averaged 1,000 m in length and were in deciduous and semi-deciduous forests, mixed coconut forest, evergreen (gallery) forest, mixed mangroves, open pastures, and plantations of *T. grandis*, *M. indica*, and mixed citrus (*Citrus* spp.). We established one transect in each habitat type; however, some transects crossed multiple habitat types. Each transect was surveyed a minimum of three times per week. Each habitat and season received the same survey effort throughout the study.

We walked transects in the morning (630–1030 hrs) and early afternoon (1400–1800 hrs) during known parrot foraging peaks (GDM, unpubl. data). Data were collected from August 2003 to July 2005. We also recorded opportunistic observations of parrots foraging at any time of day. The following data were noted whenever parrots were found feeding: date, time, habitat type, species of parrot, number of parrots, species of plant, and plant part consumed. Fruit was considered fruit pulp and not whole fruits. We ascertained whether parrots were consuming fruit pulp, seeds, or both based on evaluating dropped fruits when whole fruits were being consumed. Cultivated tree species include native and non-native trees planted by humans (usually in plantations) for the consumption of fruits and seeds, whereas non-native species refer to any species introduced to Costa Rica from another country and can include ornamentals planted for their flowers. Therefore, some species such as *M. indica* can be native and cultivated for their fruit. The two groups of islands and adjacent areas to Curú were visited sporadically, and foraging observations in these areas were recorded opportunistically. An observation of one or more parrots feeding was recorded as a single feeding bout; however, if a parrot or group of parrots flew to and fed upon another plant of the same or different species, an additional feeding bout was

recorded (Galetti 1993, Wermundsen 1997, Renton 2001).

Statistical Analyses.—The standardized Levins' (1968) niche breadth index was calculated from the number of parrots observed feeding on each plant species consumed. Values close to 0 indicates dietary specialization and a value close to 1 indicates a broad diet (Colwell and Futuyama 1971). We analyzed seasonal changes in diet by comparing the Levins' diet breadth index and number of food plant species consumed between the wet (Jun–Nov) and dry seasons (Dec–May) (Levins 1968; Renton 2001, 2006).

Pearson product-moments and simple linear regression were used to test the relationship between body mass and percent seeds, fruit pulp, flowers, and leaves in the diet using the Data Desk software package (Data Description Inc. 2006). Jaccard similarity coefficients (*J*), a statistic used to compare the similarity of plant species in the diets between psittacines, were estimated to compare the overall and seasonal diets between the five main parrot species. All data are presented as mean ± SD. All statistical tests used $\alpha = 0.05$.

RESULTS

Foraging Ecology and Diet.—We recorded 1,159 foraging bouts by six species representing all of the psittacines known from the area: Scarlet Macaw (52%), Yellow-naped Parrot (10%), White-fronted Parrot (9%), Orange-fronted Parakeet (10%), Orange-chinned Parakeet (19%), and Red-lored Parrot (<1%; Tables 1–3). Red-lored Parrots were rare at the site and only observed foraging three times; this species was eliminated from further analysis.

We observed psittacines foraging on 61 plant species from 25 families ($\bar{x} = 31 \pm 2$ plant species and $\bar{x} = 18 \pm 1.3$ plant families per psittacine species, $n = 1{,}159$ foraging bouts) (Tables 1–3). Twelve plant species were non-native and/or cultivated in Costa Rica (54% of all feeding bouts) (Tables 1–3). The number of feeding bouts per food plant species ranged from 1 to 238 ($\bar{x} = 19 \pm 35$, $n = 1{,}159$). *Terminalia catappa* (Family: Combretaceae) represented 21% of the foraging bouts. The nine next most common diet species together represented an additional 46% of the total: *Delonix regia*—9% (Family: Caesalpiniaceae), *Mangifera indica*—6% (Family: Anacardiaceae), *Tectona grandis*—6% (Family: Verbenaceae), *Pithecellobium saman*—5% (Family: Fabaceae), *Cocos nucifera*—5% (Family: Palmae), *Guazuma ulmifolia*—4% (Family: Sterculiaceae), *Elaeis guineensis*—4% (Family: Palmae), *Bombacopsis quinata*—4% (Family: Bombacaceae), and *Spondias mombin*—3% (Family: Anacardiaceae).

Psittacines ate seeds (54%), fruit pulp (24%), flowers (10%), leaves (7%), bark (4%), and lichen (<1%). Excluding Scarlet Macaws, the proportions were fruit pulp (38%), seeds (34%), and flowers (16%). All parrots consumed both ripe and unripe seeds and they fed on both cultivated and non-native species. The parrot community consumed 41 species during the wet season ($n = 572$ foraging bouts, Levins' diet breadth = 0.364) and 50 species during the dry season ($n = 587$ bouts, Levins' diet breadth = 0.205), an 18% increase in the dry season.

Scarlet Macaw.—This species ate 32 food plant species from 15 families ($n = 600$ foraging bouts, Levins' diet breadth = 0.118) (Table 1). *T. catappa* (38%) and *D. regia* (16%) were the most commonly consumed species; both are non-native. The diet was comprised of seeds (73%), fruit pulp (10%), bark (6%), flowers (5%), leaves (5%), and lichen (<1%). Non-native and cultivated plant species represented 76% of macaw foraging bouts. Macaws ate 27 food plant species in the dry season ($n = 262$ foraging bouts, Levins' diet breadth = 0.139) and 18 in the wet season ($n = 338$ foraging bouts, Levins' diet breadth = 0.216), a 33.3% increase in the dry season.

Amazona Parrots.—Yellow-naped Parrots ate 34 food plant species from 21 families ($n = 121$ foraging bouts, Levins' diet breadth = 0.388) (Table 2) and White-fronted Parrots ate 36 food plant species in 21 families ($n = 108$ foraging bouts, Levins' diet breadth = 0.225) (Table 2). The diet of Yellow-naped Parrots was comprised of seeds (61%), fruit pulp (23%), flowers (7%), leaves (7%), bark (<1%), and lichen (<1%) while the diet of White-fronted Parrots was comprised of seeds (37%), fruits (31%), flowers (26%), leaves (5%), and bark (2%). Non-native and cultivated plant species represented 37% of Yel-

TABLE 1. Foraging observations for Scarlet Macaws. Species marked with * are non-native, ** are cultivated, and *** are both non-native and cultivated. Parts eaten are coded as S = seeds, FP = fruit pulp, B = bark, L = leaves, F = flowers, and Li = lichen.

Family/Species	Part eaten	Total # individuals	Feeding bouts	Months
Anacardiaceae				
Anacardium excelsum	S	10	4	Feb–Mar
Spondias mombin	FP,B	66	27	Jul–Sep
Spondias purpurea	FP	2	1	Mar–Apr
*Mangifera indica***	FP	10	6	Feb–May
Bignoniaceae				
Tabebuia rosea	F	2	1	Feb–Mar
Bombacaceae				
Ceiba aesculifolia	F,S,B,L	9	5	Feb–Apr
Ceiba pentandra	S,B	4	2	Feb–Apr
Bombacopsis quinata	F,S,B	7	5	Dec–Feb
Ochroma pyramidale	F	12	4	Feb–May
Caesalpiniaceae				
Schizolobium parahybum	S,L,B	9	6	Apr–May
*Delonix regia**	F,S,L	206	98	Sep–Dec
Cassia grandis	F,S,B	8	4	Dec
Combretaceae				
*Terminalia catappa**	F,S,L	498	230	All year
Lythraceae				
*Lagerstroemia speciosa**	S	31	11	Oct–Jan
Meliaceae				
Cedrela odorata	S	2	1	Feb–Mar
Swietenia macrophylla	S	2	1	Jun
Fabaceae				
Pseudosamanea guachapele	F,L,B	23	9	Nov
Lysiloma divaricatum	S	7	3	Jan–Mar
Enterolobium cyclocarpum	B,Li	4	2	Feb–Mar
Inga vera	F,S,L	18	4	Mar–May
Inga sp.	S	5	6	Mar–Apr
Pithecellobium saman	F,S,L,B	56	42	Jan–Mar
Moraceae				
Ficus sp.	F,S,FP	2	1	Oct
Myrtaceae				
*Psidium guajava***	F,S,FP,L	19	5	Mar–Apr
Palmae				
*Cocos nucifera**	S	92	55	All year
*Elaeis guineensis****	F	30	14	Jul–Sep
Rhizophoraceae				
Rhizophora mangle	B,L	5	4	Sep
Sterculiaceae				
Sterculia apetala	S	2	1	Mar
Guazuma ulmifolia	F	12	7	Dec–Feb
Tiliaceae				
Luehea seemannii	F,S	9	4	Jan–Feb
Verbenaceae				
*Tectona grandis****	S,L	76	31	Sep–Nov
Avicennia germinans	S	6	6	Sep
Total # individuals and bouts		1,244	600	

low-naped Parrot foraging bouts, while non-native and cultivated plant species represented 24.1% of White-fronted Parrot foraging bouts.

Yellow-naped Parrots ate 18 plant species in the wet season (n = 61, Levins' diet breadth = 0.373) and 23 in the dry season (n = 60, Levins' diet breadth = 0.370), a 21.7% increase in the dry season. White-fronted Parrots ate 22 plant species in the wet season (n = 44, Levins' diet breadth = 0.160) and 26 in the dry season (n = 64, Levins' diet breadth = 0.417), a 15.4% increase in the dry season.

Parakeets.—Orange-fronted Parakeets ate 24 food plant species in 16 families (n = 113 foraging bouts, Levins' diet breadth = 0.551) (Table 3) and Orange-chinned Parakeets ate 30 food plant species in 17 families (n = 214 foraging bouts, Levins' diet breadth = 0.244) (Table 3). The diet of Orange-fronted Parakeets was comprised of fruits (47%), seeds (25%), flowers (20%), leaves (6%), and bark (3%) while the diet of Orange-chinned Parakeets was comprised of fruits (47%), seeds (20%), leaves (15%), flowers (14%), and bark (4%). Non-native and cultivated plant species represented 33% of Orange-chinned Parakeets foraging bouts, while non-native and cultivated plant species represented 17% of the foraging bouts of Orange-fronted Parakeets.

Orange-fronted Parakeets ate 14 plant species in the wet season (n = 39, Levins' diet breadth = 0.574) and 17 in the dry season (n = 74, Levins' diet breadth = 0.580), a 17.6% increase in the dry season. Orange-chinned Parakeets ate 19 plant species in the dry season (n = 124, Levins' diet breadth = 0.175) and 23 in the wet season (n = 90, Levins' diet breadth = 0.361), a 17.4% decrease in the dry season.

Diet Similarities.—Overall diet overlap was greater (J range 52–71.4) than diet overlap when compared in the dry and wet seasons (J dry range 26.1–57.1, J wet season range 26.3–46.2). The greatest overall similarity in psittacine diets was between Orange-chinned Parakeets and Scarlet Macaws (J = 71.4) and Orange-fronted Parakeets (J = 66.7), and between both *Amazon* parrots (J = 65.2). Seasonally, the greatest similarity in psittacine diets was in the wet season between Orange-chinned Parakeets and White-fronted Parrots (J = 56) and Orange-fronted Parakeets (J = 57.1), and between White-fronted Parrots and Orange-fronted Parakeets (J = 52.4). In the dry season, the greatest similarity in diets was between Orange-chinned Parakeets and Scarlet Macaws (J = 46.2) and White-fronted Parrots (J = 45), and between Orange-fronted Parakeets and Scarlet Macaws (J = 43.5).

Body Type and Food Type Preference.—There was a significant positive correlation between body mass and percent seeds in the diet (r = 0.97, P = 0.008), and a significant negative correlation between body mass and percent fruit pulp in the diet (r = −0.96, P = 0.009, Fig. 1). Body mass did not correlate with either the percent of flowers (r = −0.71, P = 0.179) or percent of leaf consumption (r = −0.48, P = 0.42) in the diet of this parrot community.

DISCUSSION

Foraging Ecology and Diet.—The Costa Rican parrot community studied ate predominantly seeds (54% of all foraging observations). This confirms the general characterization of parrots as major seed predators (Desenne 1994, Renton 2001). However, when Scarlet Macaws were excluded, parrots in our study consumed more fruit pulp and flowers than seeds. This was due to the smaller-bodied species consuming more fruit and flowers than seeds, as reported in other parrot communities (Desenne 1994, Pizo et al. 1995).

All parrots in Curú foraged on flowers (5–26% of their diets). This is a larger percentage of flowers than reported by most studies: Renton (2001) found that Lilac-crowned Parrots (*Amazona finschi*) do not consume flowers in Mexico; flowers comprised only 4.1% of the diet of the Pacific Parakeet (*Aratinga strenua*) in Nicaragua (Wermundsen 1997); and flowers were only 2.5% of the diet of Puerto Rican Amazons (*Amazona vittata*) (Snyder et al. 1987). Desenne (1994) and Pizo et al. (1995) documented that flowers comprised 18% of all foraging bouts in two parrot communities, while Galetti (1993) found that flowers comprised 20% of the diet of Scaly-headed Parrots (*Pionus maximiliani*) and Pizo et al. (1995) reported that flowers comprised 25% of the diet of Reddish-bellied Parakeets (*Pyrrhura frontalis*). Flower consumption is important because some psittacines reportedly act as pollinators (Cotton 2001), while many destroy the flowers they eat (Ragusa-Netto 2005;

TABLE 2. Foraging observations for Yellow-naped and White-fronted parrots. Species marked with * are non-native, ** are cultivated, and *** are both non-native and cultivated. Parts eaten are coded as S = seeds, FP = fruit pulp, B = bark, L = leaves, F = flowers, and Li = lichen.

Family/Species	Part eaten	Yellow-naped Parrot		White-fronted Parrot		Months
		# ind.	# bouts	# ind.	# bouts	
Anacardiaceae						
Anacardium excelsum	S	2	1	6	3	Mar–Apr
Spondias mombin	FP	40	6	10	2	Aug–Sep
*Mangifera indica***	FP,L	15	6	18	8	Mar
Astronium graveolens	S	0	0	2	1	Mar
Annonaceae						
Annona sp.	FP	4	1	0	0	Feb
Bignoniaceae						
Tabebuia rosea	F	4	2	4	2	Feb–Mar
Bombacaceae						
Ceiba pentandra	S,L,B	0	0	4	3	Feb
Bombacopsis quinata	F,FP,S	33	11	0	0	Feb–Apr
Ochroma pyramidale	F	0	0	2	1	Jan
Boraginaceae						
Cordia alliadora	S,F	2	1	3	2	Feb
Burseraceae						
Bursera simaruba	S	50	8	9	4	Feb–Mar
Caesalpiniaceae						
Schizolobium parahybum	F,L	9	4	5	2	Apr–May
Senna reticulata	S	0	0	5	1	Feb
Tamarindus indica	S	0	0	2	1	Feb
Chrysobalanaceae						
Licania platypus	L	2	1	0	0	Jan
Combretaceae						
*Terminalia catappa**	S	8	1	17	4	Feb–Mar
Terminalia oblonga	S	2	1	3	1	Feb
Combretum sp.	F	3	2	0	0	Feb
Elaeocarpaceae						
Muntingia calabura	S,FP	12	1	0	0	Jan
Euphorbiaceae						
Sapium glandulosum	S,FP	9	3	10	1	Sep–Oct
Leguminocae						
Erythrina poeppigiana	F	4	2	35	9	Dec–Jan
Erythrina costaricensis	F	5	1	2	1	Jan–Feb
Lorantaceae						
Psittacamthus sp.	S,F	0	0	10	3	Oct–Dec
Meliaceae						
Cedrela odorata	S,FP	29	5	2	1	Feb–Mar
Fabaceae						
Lysiloma divaricatum	S	4	2	4	2	Mar–Apr
Enterolobium cyclocarpum	S,L,B,Li	19	7	5	2	Feb–Apr
Inga sp.	S,F,B	0	0	10	4	Jul
Pithecellobium saman	S,F,L	0	0	7	3	Mar
Leucaena leucocephala	S	21	7	5	2	Jun–Sep

TABLE 2. Continued.

Family/Species	Part eaten	Yellow-naped Parrot		White-fronted Parrot		Months
		# ind.	# bouts	# ind.	# bouts	
Moraceae						
Brosimum alicastrum	S,FP	0	0	45	1	Oct
Ficus insipida	S,FP	12	2	19	2	Oct
Myrtaceae						
*Psidium guajava***	S,FP	3	1	0	0	Apr
Palmae						
Scheelea rostrata	FP	4	2	0	0	Jun, Sep
*Elaeis guineensis****	FP	0	0	145	8	May–Jun
Rhizophoraceae						
Rhizophora mangle	F	0	0	4	1	Jan
Rubiaceae						
Calycophyllum candidissimun	S	6	1	0	0	Feb
Rutaceae						
*Citrus aurantifolia****	S	10	2	0	0	Oct–Nov
*Citrus limeta****	S	6	2	0	0	Nov
*Citrus aurantium****	S	49	17	17	2	Oct–Dec
*Citrus paradise****	S	2	1	0	0	Nov
Zanthoxylum sp.	S,FP	8	1	2	1	Sep
Sterculiaceae						
Sterculia apetala	S	0	0	2	1	Feb–Mar
Guazuma ulmifolia	S,FP	1	1	23	9	Nov–Jan
Tiliaceae						
Luehea seemannii	S,F	4	1	33	11	Dec–Jan
Verbenaceae						
*Tectona grandis****	S	67	16	15	4	Aug–Nov
Avicennia germinans	S,L	4	1	11	4	Apr–Sep
Unknown Vine sp.	S	0	0	5	1	Feb
Total # individuals and bouts		453	121	501	108	

GDM, unpubl. data). Given that parrots and other flower eaters can destroy the entire flower crop of individual trees (Galetti 1993, Ragusa-Netto 2005), it is important for researchers to be aware of the possible ecological impacts of lowering fitness of these plant species in heavily modified landscapes where tree abundances of some species may have been drastically lowered by habitat clearing.

The relationship between parrot body size and the percentage of seeds or fruit in the diet may be related to nutritional requirements of parrot species. Seeds are generally high in protein (Gilardi 1996) and larger-bodied avian species may require greater amounts of protein for maintenance (Klasing 1998). Smaller-bodied species may require more fruit pulp, which can be high in sugars, as their metabolism may require additional energy since they have higher energy needs than larger-bodied species. Therefore, the abundance and ratios of larger-bodied and smaller-bodied parrots in a psittacine community may be a good predictor of what plant species may be required to sustain populations in certain areas.

The small-bodied parakeets and *Amazona* parrots showed the most similarity in overall psittacine diets, suggesting that congeneric and similar-sized species forage on a large subset of the same plant species. The greater similarity in psittacine diets in the wet season as opposed to the dry season could be related to fewer species of trees producing parrot food in the wet season (Matuzak and Brightsmith 2007) making it more likely that psittacines would forage on the same plant species.

TABLE 3. Foraging observations for Orange-fronted and Orange-chinned parakeets. Species marked with * are non-native, ** are cultivated, and *** are both non-native and cultivated. Parts eaten are coded as S = seeds, FP = fruit pulp, B = bark, L = leaves, F = flowers, and Li = lichen.

Family/Species	Part eaten	Orange-fronted Parakeet		Orange-chinned Parakeet		Months
		# ind.	# bouts	# ind.	# bouts	
Anacardiaceae						
Anacardium excelsum	F	0	0	2	1	Feb
Spondias mombin	FP	12	2	21	2	Sep
Spondias purpurea	L	3	1	0	0	Oct
*Mangifera indica***	FP	4	1	532	47	May–Aug
Bignoniaceae						
Tabebuia rosea	F,L,B	8	4	17	5	Apr, Jun
Bombacaceae						
Ceiba aesculifolia	S,F	0	0	14	8	Jan–Apr
Ceiba pentandra	S,F,L,B	0	0	172	11	Feb–Apr
Bombacopsis quinata	S,F,L,B	23	5	100	22	Jan–Apr
Caesalpiniaceae						
Schizolobium parahybum	L	0	0	8	1	Jul
*Delonix regia**	F	8	1	2	1	Jun
Senna sp.	F	2	1	20	1	Mar
Cecropiaceae						
Cecropia sp.	S,F	0	0	6	2	Jul
Combretaceae						
*Terminalia catappa**	F	28	3	0	0	Dec
Terminalia oblonga	S	2	1	0	0	Feb
Laguncularia racemosa	L	0	0	73	8	Feb–May
Euphorbiaceae						
Sapium glandulosum	FP	7	2	15	2	Aug–Oct
Leguminocae						
Gliricidia sepium	S,F	15	7	0	0	Jan–Feb
Erythrina poeppigiana	F	4	1	0	0	Jan
Lorantaceae						
Psittacamthus sp.	S,F	6	2	31	6	Sep–Oct
Meliaceae						
Cedrela odorata	S,FP,L,B	34	8	11	2	Sep–Oct
Swietenia macrophylla	S	0	0	4	1	Nov
Fabaceae						
Enterolobium cyclocarpum	L,B	12	1	67	8	Mar–Aug
Inga vera	F	0	0	3	1	Feb
Pithecellobium saman	S,F,L	10	2	88	11	Jan–Feb
Moraceae						
Brosimum alicastrum	S,FP	0	0	14	4	Jun
Ficus insipida	S,FP,B	0	0	209	12	May–Jul
Myrtaceae						
*Psidium guajava***	S,FP	25	7	60	10	Mar–Apr
Palmae						
*Elaeis guineensis****	FP	18	3	156	19	Jun–Jul
Rutaceae						
Zanthoxylum sp.	S,FP	16	3	16	5	Jun–Aug

TABLE 3. Continued.

Family/Species	Part eaten	Orange-fronted Parakeet # ind.	Orange-fronted Parakeet # bouts	Orange-chinned Parakeet # ind.	Orange-chinned Parakeet # bouts	Months
Sterculiaceae						
Sterculia apetala	S	22	2	46	7	Jan–Feb
Guazuma ulmifolia	S,FP	115	32	3	2	Dec–Apr
Tiliaceae						
Luehea seemannii	S,F	5	2	4	1	Jan, Jun
Verbenaceae						
*Tectona grandis****	S,F	36	11	15	3	Jun–Sep
Verbenaceae						
Avicennia germinans	S,L	57	11	29	5	Aug–Sep
Unknown Vine sp.	S	0	0	31	6	Jan–Feb
Total # individuals and bouts		472	113	1,869	214	

Smaller parrot species such as those in *Brotogeris* and *Aratinga* often increase in abundance in modified landscapes, as larger parrot species decline (Karubian et al. 2005). Thus, anthropogenic impacts can drastically reduce the ratio of large to small psittacines in a community. Smaller-bodied parrot species may even disperse some smaller-seeded trees (Janzen 1981, Fleming et al. 1985). Plant reproduction and regeneration in modified landscapes could be altered by removing the largest-bodied seed predators, and increasing floral predators and potential dispersers of small seeds.

Diet Specialization and Seasonal Shifts.—The number of plant types consumed by each parrot species ranged from 24 to 36 species from 15 to 21 plant families. The numbers of food items consumed by the two *Amazona* species in Curú are similar to those for other parrot species: Scaly-headed Parrots in Brazil ate 38 plant species from 18 families (Galetti 1993) and Lilac-crowned Parrots in Mexico ate 33 plant species from 14 families (Renton 2001). Orange-fronted Parakeets in Curú foraged on 24 food plant species in 16 families. This is greater than the 15 species from 12 families recorded for the congeneric Pacific Parakeet in Nicaragua (Wermundsen 1997). Scarlet Macaws foraged on 32 food plant species in 15 families in Curú, while studies of wild Scarlet Macaws reported 15, 43, and 52 food species in Belize; Carara, Costa Rica; and Peru, respectively (Gilardi 1996, Renton 2006, Vaughan et al. 2006).

Diet composition of each species of parrot varied seasonally. Four of five parrot species ate more plant species during the dry season than the wet season. This trend corresponds with an increase in the number of food species available, and the percentage of trees bearing seeds and flowers during the dry season (GDM, unpubl. data). The number of food species and trees bearing large quantities of fruit pulp such as *M. indica*, *S. mombin*, *E. guineensis*, *Psidium guajava*, and *Scheelea rostrata* increased during the wet season. The wet season was also when leaves became a larger part of the diet of each species.

Diet breadth among parrots usually increases with increasing food abundance and diversity of available food items (Wermundsen 1997, Renton 2001). This pattern held for only one species in our study, White-fronted Parrot, which had a 260% increase in diet breadth when food availability peaked in the dry season (Matuzak and Brightsmith 2007). The increase in diet breadth of Orange-chinned Parakeets during the wet season could also be related to food abundance, as fruit pulp (the species preferred food part) abundance peaks at this time of year (GDM, unpubl. data). Two other species, Scarlet Macaws and Orange-chinned Parakeets, had more specialized diets during the dry season food peak (36 and 52% reductions in diet breadth, respectively). During the dry season in Belize, Scarlet Macaws have a less specialized diet (Levins' diet breadth = 0.394; Renton 2006) than did Scarlet Macaws in our study (Levins' diet breadth

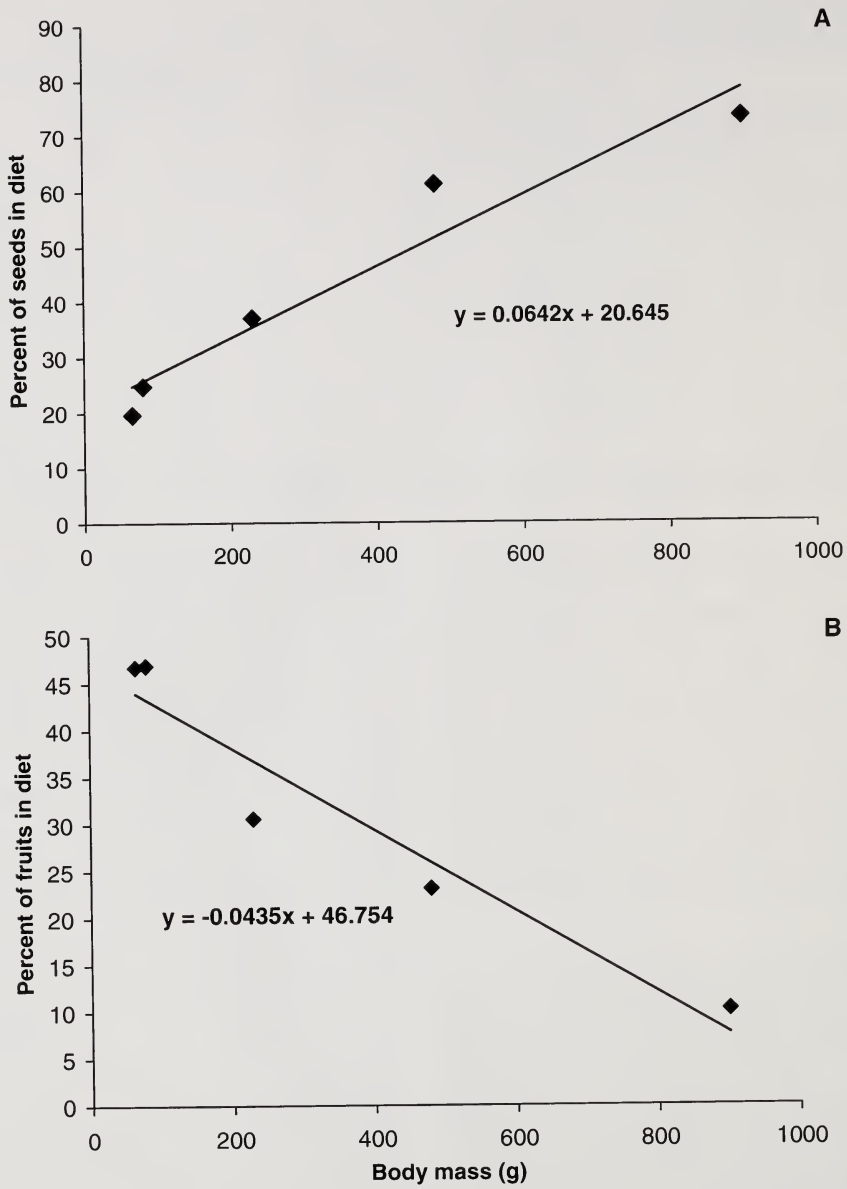


FIG. 1. Body mass versus percent of seeds (A) and fruits (B) in the diets of parrots in Curú Wildlife Refuge on the Nicoya Peninsula of Costa Rica.

= 0.139). In Curú, Scarlet Macaws in the dry season specialize on two food items, *P. saman* and *T. catappa*, both of which produce abundant resources in the dry season and combine for 53% of the macaws' dry season diet. The more specialized diet of macaws in this study may be due to several factors, including less food diversity and availability due to a human modified landscape, a preference for *T. catappa* over other available resources, and/or a lack of knowledge and training to find local resources after their release to the site. The diet breadth of Lilac-crowned Amazons in Mexico was 0.22 in the dry season and 0.55 in the wet season when the number of food species available peaked (Renton 2001). The diet breadth of the two species of *Amazona* parrots in Curú was larger in the dry season

and lower in the wet season when compared to Lilac-crowned Amazons; however, food availability peaked in the dry season in Curú. Yellow-naped Parrots and Orange-fronted Parakeets exhibited no major difference in diet breadth between seasons.

Native versus Non-native Food Plant Species.—Use of non-native food resources by parrots is widespread and important in sustaining some species during times of low food availability (Forshaw 1989, Pitter and Christiansen 1995). Over half of all foraging bouts in our study were on non-native and cultivated tree species; however, when macaws are not included, only 29% of foraging bouts were on non-native and cultivated species. Non-native species consumed included two naturalized species that occur along the coasts of Costa Rica (*C. nucifera* and *T. catappa*), seven species cultivated for fruit (4 species of *Citrus*, *M. indica*, *P. guajava*, and *E. guineensis*), two non-native ornamentals (*D. regia* and *Lagerstroemia speciosa*), and *T. grandis*, a tree planted for timber (Holdridge et al. 1997).

Two species (*C. nucifera* and *T. catappa*) were used mainly by Scarlet Macaws and represented 48% of their diet. Wild populations of macaws at other sites in Costa Rica forage heavily on *T. catappa* as this plant species is highly abundant and is in seed all year along coastal areas and beaches where wild macaws are found. The macaws in Curú exploit a similar range of food resources in similar environments as wild macaws along the central coast of Costa Rica (Vaughan et al. 2006; GDM, unpubl. data).

Citrus trees (lime, lemon, grapefruit, and orange) were an important food resource for Yellow-naped Parrots from November to December, a period of increasing food abundance prior to onset of nesting (Matuzak and Brightsmith 2007). Two species, *E. guineensis* and *T. grandis*, provided important food resources for the entire parrot community. These species were important during declining food availability and low food diversity, April–June and September–October, respectively (Matuzak and Brightsmith 2007).

CONSERVATION IMPLICATIONS

The ability of psittacines to exploit non-native resources may be important for their future survival, not only in Costa Rica, but across Latin America. The high rates of habitat conversion in Costa Rica over the past several decades have produced millions of hectares dominated by forest fragments, small farms, and plantations (Kleinn et al. 2002). Parrots have greatly expanded their available food base by using introduced and cultivated food plants. As more areas of the Neotropics are converted from native habitats to small farms, persistence of parrots may become linked to their ability to exploit introduced and cultivated species in modified landscapes.

Use of non-native and cultivated species brings psittacines into direct competition with humans, making them a perceived pest of crops (Bucher 1992). Psittacines in many parts of the world are trapped or killed due to real or perceived damage to crops (Bucher 1992). The benefits of feeding on introduced and cultivated species for most psittacines apparently outweigh the mortality inflicted by humans and, as a result, some species become abundant in modified landscapes (Pitter and Christiansen 1995, Moegenburg and Levey 2003). However, for uncommon psittacines with low reproductive rates like macaws or large amazons, conflicts with humans could threaten the species' persistence (Bucher 1992).

Deforestation in Costa Rica has removed up to 60–70% of the nation's original forest cover (Kleinn et al. 2002). In the study area, many hectares are regenerating forest cover as farms and pastures are being abandoned (Kleinn et al. 2002). Targeted restoration of *G. ulmifolia*, *B. quinata*, *S. mombin*, and *L. seemannii* in our study area would be feasible and of great benefit as these native tree species provide key food resources to psittacines. *G. ulmifolia* and *S. mombin* are of special importance since both fruit during the time of lowest overall food availability and may turn out to be keystone species in these dry forest environments. Increasing the abundance of native species should also decrease the dependence of psittacines on introduced and cultivated species, and decrease the potential for negative interactions with humans.

ACKNOWLEDGMENTS

We thank Agustina Arcos, Alejandro Solano, Laura Palasz, Sigrid Collado, Olivier Horiot, Jerome Hillaire, Cynthia Shafer, and all project assistants and volunteers for their dedication to assisting with the field-

work. We thank Jason May for helping with statistical analyses and the Ministry of Environment and Energy (MINAE) in Costa Rica and the Curú Wildlife Refuge for their support of the project and access to all areas of the wildlife refuge. Funding was provided by Amigos de las Aves USA Parrot Conservation and Research Fund, The Amazona Society, Loro Parque Foundation, Lincoln Park Zoo, Bird Clubs of Virginia, Columbus Zoo, Kaytee Avian Foundation, Cleveland Zoological Society, and the following private donors: Tracey Coryell, Jeff Kidston, and Dr. Janice Boyd.

LITERATURE CITED

Bennett, P. M. and I. P. F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings of the Royal Society of London B. 264:401–408.

Brightsmith, D., J. Hilburn, A. del Campo, J. Boyd, M. Frisius, R. Frisius, D. Janik, and F. Guillen. 2005. The use of hand-raised psittacines for reintroduction: a case study of Scarlet Macaws (*Ara macao*) in Peru and Costa Rica. Biological Conservation 121:465–472.

Bucher, E. H. 1992. Neotropical parrots as agricultural pests. Pages 201–219 *in* New World parrots in crisis: solutions from conservation biology (S. R. Beissinger and N. F. R. Snyder, Editors). Smithsonian Institute Press, Washington, D.C., USA.

CITES. 2002. Transfer the Yellow-naped Amazon (*Amazona auropalliata*) from Appendix II to Appendix I. Proponent: Costa Rica. Conference of the Parties to the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES). Proposition 16.

Collar, N. J. 1997. Family Psittacidae. Pages 280–479 *in* Handbook of the birds of the world (J. del Hoyo, A. Elliott, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

Collar, N. J. 1998. Information and ignorance concerning the word's parrots: an index for twenty-first century research and conservation. Papageienkunde 2:201–235.

Colwell, R. K. and D. J. Futuyama. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

Cotton, P. A. 2001. The behavior and interactions of birds visiting *Erythrina fusca* flowers in the Colombian Amazon. Biotropica 33:662–669.

Data Description Inc. 2006. Data Desk statistical software. Ithaca, New York, USA.

Desenne, P. 1994. Estudio preliminar de la dieta de 15 especies de psitacidos en un bosque siempreverde, cuenca del Rio Tawadu, Reserva Forestal El Caura, Edo. Bolivar. Pages 25–42 *in* Biología y conservación de los psitácidos de Venezuela (G. Morales, I. Novo, D. Bigio, A. Luy, and F. Rojas-Suarez, Editors). Graficas Giavimar, Caracas, Venezuela.

Fleming, T. H., C. F. Williams, F. J. Bonaccorso, and L. H. Herbst. 1985. Phenology, seed disperal, and colonization in *Muntingia calabura*, a neotropical pioneer tree. American Journal of Botany 72:383–391.

Forshaw, J. M. 1989. Parrots of the world. Third Edition. Landsdowne Editions, Melbourne, Australia.

French, A. R. and T. B. Smith. 2005. Importance of body size in determining dominance hierarchies among diverse tropical frugivores. Biotropica 37: 96–101.

Galetti, M. 1993. Diet of the Scaly-headed Parrot (*Pionus maximiliani*) in a semi-deciduous forest in southeastern Brazil. Biotropica 25:419–425.

Gilardi, J. D. 1996. Ecology of parrots in the Peruvian Amazon: habitat use, nutrition and geophagy. Dissertation. University of California, Berkeley, USA.

Holdridge, L. R., L. J. Poveda, and Q. Jimenez. 1997. Arboles de Costa Rica. Volume 1. Tropical Science Center, San Jose, Costa Rica.

Janzen, D. H. 1981. Seed predation by Orange-chinned Parakeets in Costa Rica. Auk 98:841–844.

Karubian, J., J. Fabara, D. Yunes, J. P. Jorgenson, D. Romo, and T. B. Smith. 2005. Temporal and spatial patterns of macaw abundance in the Ecuadoran Amazon. Condor 107:617–626.

Klasing, K. C. 1998. Comparative avian nutrition. CAB International, Wallingford, Connecticut, USA.

Kleinn, C., L. Corrales, and D. Morales. 2002. Forest area in Costa Rica: a comparative study of tropical forest cover estimates over time. Environmental Monitoring and Assessment 73:17–40.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.

Matuzak, G. D. and D. J. Brightsmith. 2007. Roosting of Yellow-naped Parrots in Costa Rica: estimating the size and recruitment of threatened populations. Journal of Field Ornithology 78:159–169.

Moegenburg, S. M. and D. J. Levey. 2003. Do frugivores respond to fruit harvest? An experimental study of short-term responses. Ecology 84:2600–2612.

Munshi-South, J. and G. S. Wilkinson. 2006. Diet influences life span in parrots (Psittaciformes). Auk 123:108–118.

Pitter, E. and M. B. Christiansen. 1995. Ecology, status and conservation of the Red-fronted Macaw (*Ara rubrogenys*). Bird Conservation International 5:61–78.

Pizo, M. A., I. Simao, and M. Galetti. 1995. Diet and flock size of sympatric parrots in the Atlantic forest of Brazil. Ornitologia Neotropical 6:87–95.

Ragus-Netto, J. 2005. Extensive consumption of *Tabebuia aurea* (Manso) Bentham & Hooker (Bignoniaceae) nectar by parrots in a tecoma savanna in the southern Pantanal (Brazil). Brazilian Journal of Biology 65:339–344.

Renton, K. 2001. Lilac-crowned Parrot diet and food

resource availability: resource tracking by a parrot seed predator. Condor 103:62–69.

Renton, K. 2006. Diet of adult and nestling Scarlet Macaws in southwest Belize, Central America. Biotropica 38:280–283.

Sazima, I. 1989. Peach-fronted Parakeet feeding on winged termites. Wilson Bulletin 101:656–657.

Schutt, A. and C. Vaughn. 1995. Incorporating wildlife into development: the case of the Curu wildlife refuge and farm, Costa Rica. Pages 250–254 *in* Integrating people and wildlife for a sustainable future. Proceedings of the First International Wildlife Management Congress (J. A. Bissonette and P. R. Krausman, Editors). The Wildlife Society. Bethesda, Maryland, USA.

Snyder, N. R. F., J. W. Wiley, and C. B. Kepler. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, California, USA.

Stiles, F. G. and A. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

Tosi, J. 1969. Ecological life zone map of Costa Rica. Tropical Science Center, San Jose, Costa Rica.

Vaughan, C., N. Nemeth, and L. Marineros. 2006. Scarlet Macaw, *Ara macao*, (Psittaciformes: Psittacidae) diet in central Pacific Costa Rica. International Journal of Tropical Biology 54:919–926.

Vaughan, C., J. F. Gamboa, D. Hernandez, J. M. Mora, P. E. Sanchez, and H. C. Kiel. 1994. Evaluacion de los recursos biologicos y diseno de corredores para los distritos de Lepanto, Paquera, y Cobano del Canton Central de la Provincia de Puntarenas. Informe Final. Universidad Nacional, Heredia, Costa Rica.

Wermundsen, T. 1997. Seasonal change in the diet of the Pacific Parakeet *Aratinga strenua* in Nicaragua. Ibis 139:566–568.

The Wilson Journal of Ornithology 120(2):366–370, 2008

THE SIGNAL FUNCTION OF A MELANIN-BASED PLUMAGE ORNAMENT IN GOLDEN-WINGED WARBLERS

EMILY ANNE McKINNON[1,2,3] AND RALEIGH J. ROBERTSON[1]

ABSTRACT.—The decline of Golden-winged Warblers (*Vermivora chrysoptera*) has been attributed in part to hybridization with a sister species, the Blue-winged Warbler (*V. pinus*), which lacks the black throat patch typical of the Golden-winged Warbler. Understanding the signal function of male plumage ornaments in Golden-winged Warblers may provide insight into the mechanisms driving hybridization. If Golden-winged Warbler males use the black throat patch for interspecific signaling, Blue-winged Warblers or hybrids may be leading hybridization between the species. We examined the signal function of the melanin-based throat patch in a population of Golden-winged Warblers on the edge of the hybrid zone. Males with increased ultra violet chroma in their throat patches were older and their mates had significantly earlier first egg dates. This suggests the black throat patch of Golden-winged Warblers may be an age-related indicator of quality. Female Golden-winged Warblers should not mate preferentially with males which lack the black throat patch if it functions as an indicator of age and or male quality. *Received 13 January 2007. Accepted 22 September 2007.*

Females, in many birds that exhibit sexual dimorphism, prefer and benefit from choosing more ornamented and older mates (Andersson 1994). Sexually selected plumage may have a role in maintaining species separation in sympatric populations of related species (Saetre et al. 1997). Golden-winged (*Vermivora chrysoptera*) and Blue-winged (*V. pinus*) warblers are sister species that regularly hybridize in areas of range overlap (Gill 1997), yet hybridization seems to result in the eventual extirpation of the Golden-winged Warbler (Gill 1980). Reasons for this are unclear; recent work (Leichty and Grier 2006) suggests that non-assortative mate choice based on plumage may contribute to genetic swamping of Golden-winged Warblers by Blue-winged Warbler genes.

Golden-winged Warblers have a black, melanin-based throat patch and auriculars, and a carotenoid-based yellow cap and wingbar. Blue-winged Warblers are yellow overall with grayish-blue wings and a thin black eye-line. Hybrid females generally resemble female Golden-winged Warblers and not Blue-winged Warblers. Thus, male Golden-winged Warblers may pair with hybrid females, while male Blue-winged Warblers are less likely to pair with a hybrid (Confer 2006). Leichty and Grier (2006) experimentally found that female Golden-winged Warblers do not pair with simulated hybrids (males with facial pattern experimentally removed). This suggests the black facial pattern is an important species-specific signal for mate choice. Leichty and Grier (2006) also reported that males lacking the black facial pattern lost their territory more often than untreated Golden-winged Warblers, suggesting the throat patch may function in intrasexual interactions.

Our objectives were to: (1) describe reflectance characteristics of the Golden-winged Warbler throat patch, and (2) ascertain if these characteristics correlated with indices of male quality, which would suggest a possible signal function. Reproductive success and age were used as indicators of male quality. We recorded the date a male's mate first laid an egg as a proxy for reproductive success. We expected ultra violet (UV) chroma (proportion of reflectance in the UV range) and darkness to be important components of the melanin-based patch (Mennill et al. 2003). If the black throat patch functions as a signal of fitness, high quality throat patches should correlate with increased reproductive success. Throat patch quality should also increase with age (Brooks and Kemp 2001).

METHODS

We captured 34 male Golden-winged Warblers (18 after-second year, ASY; and 16 second-year, SY) with mist nets from 6 May to

[1] Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada.

[2] Current address: Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, NB E3B 6E1, Canada.

[3] Corresponding author;
e-mail: emily_anne.mckinnon@unb.ca

15 July 2005 at the Queen's University Biological Station (44° 34′ N, 76° 19′ W; 40 km north of Kingston, Ontario, Canada). This population of Golden-winged Warblers is on the edge of the hybrid zone (Dabrowski et al. 2005). Arriving Golden-winged Warblers were monitored at known breeding sites and first egg date was recorded for each pair's first nest ($n = 11$) for those territories where we were able to find the nest.

Three throat patch feathers were collected from each male and stored in opaque envelopes until analysis. Feathers from each bird were taped to dark black paper with less than 10% reflectance (CANSON #425 Stygian black) overlapping in a way that mimicked how they would lay on the bird. Plumage coloration was measured in a darkened laboratory room with no windows (to minimize variation in ambient light) using an Ocean Optics S2000 spectrometer with a PX-2 pulsed xenon lamp set to a white spectralon standard (WS-1) (Ocean Optics Inc., Dunedin, FL, USA) and dark standard (black felt in a box). A rubber sheath fitted over the spectrometer probe excluded light and ensured the probe was at a fixed distance, perpendicular to the sample. Five readings from each sample (lifting and lowering the probe between readings) were repeatable ($r = 0.61$, $F_{34,140} = 8.95$, $P < 0.001$) (Lessells and Boag 1987) and were averaged for analyses. Analysis was limited to wave lengths from 300 to 700 nm, the approximate visual range of passerines (Cuthill et al. 1999). Average reflectance for each 10-nm interval from 300 to 700 nm was calculated to give 41 reflectance measures per bird.

Reflectance data were summarized using principal components analysis (PCA). All data conformed to assumptions of parametric statistics. Principal components (PCs) were compared to first egg date with linear regressions. Throat patch components were compared between age classes (ASY and SY) with two-sample *t*-tests. All statistics were calculated using JMP 5.1.

RESULTS

Principal component I proved to be a measure of "darkness" of the throat patch. It represented reflectance across all wave lengths equally, as confirmed by a strong positive relationship when plotted against mean reflectance ($r = 0.99$, $P < 0.001$, $n = 34$). Principal component II was a measure of "UV chroma" of the throat patch and correlated positively ($r = 0.96$, $P < 0.001$, $n = 34$) with the proportion of reflectance in the UV range. The eigenvalue for PC II was < 1, but we retained PC II in the analyses. Principal component III explained 0.5% of the variation, representing variation at short (UV) and long (red) wave lengths. Only PCs I and II were considered in the following tests due to the small influence of PC III on variation in spectra, and with no clear biological reason to support addition of PC III to the analyses.

Throat patch plumage had low reflectance with little variation across the spectrum examined (Fig. 1). PC I scores of older (ASY) males did not differ significantly from PC I scores of second-year (SY) males ($t = 2.03$, $P = 0.20$, $n = 18$ and 16) although, on average, their throat patches were darker than those of younger males (Fig. 2A). Older males had higher PC II scores than younger males ($t = 2.03$, $P = 0.034$, $n = 18$ and 16) (Fig. 2B) indicating they had a greater proportion of UV reflectance in their throat patch than younger males.

Principal component I did not correlate with first egg date ($r = 0.22$, $P = 0.51$, $n = 11$); however, PC II and first egg date had a significant negative trend ($r = -0.65$, $P = 0.029$, $n = 11$) (Fig. 3) indicating that males with higher UV reflectance in their throat patch generally had mates which laid eggs earlier in the season.

DISCUSSION

Throat patch feathers of male Golden-winged Warblers had a reflectance curve similar to that of Black-capped Chickadees (*Poecile atricapillus*) (Mennill et al. 2003) with some variation at UV wave lengths and little variation across the rest of the spectrum (Fig. 1). Our PCA results suggest that UV chroma (PC II) and darkness (PC I) account for the majority of the variation across male Golden-winged Warbler throat patches. Males with the highest UV chroma had mates that laid eggs significantly earlier in the season. Earlier first egg dates are positively correlated with increased reproductive success in other species (Verhulst et al. 1995). This suggests UV chro-

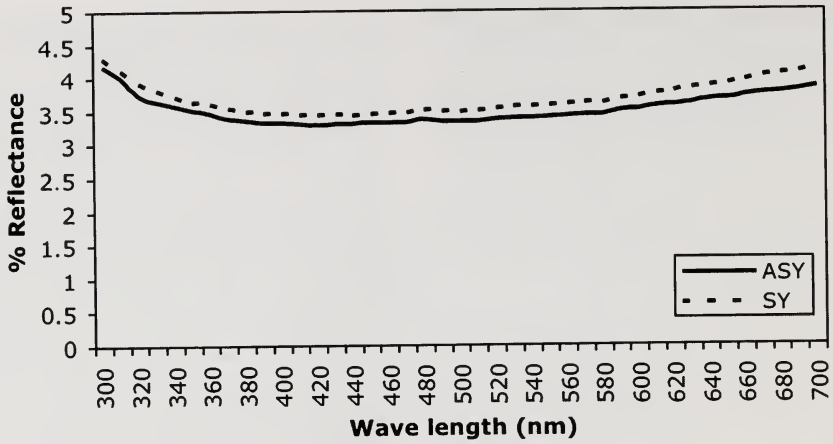


FIG. 1. Golden-winged Warbler plumage reflectance curves for the throat patch of ASY (solid line) and SY (dashed line) males. Curves were calculated from average reflectance values.

ma and reproductive success may be positively correlated in Golden-winged Warblers.

The darkness of the throat patch did not correlate significantly with first egg date or age. It may be that darkness is not as important as a signal as UV chroma. However, analysis of feathers in the laboratory has limitations in how it can be applied to reflectance of feathers on a living bird. The background paper may have shown through the feathers influencing darkness measurements by increasing their reflectance. This problem would have affected darkness more than UV chroma, as the paper did not reflect in UV wave lengths. Mounting feathers on different backgrounds with varying reflectance, although beyond the scope of this study, would allow the magnitude of this effect to be examined.

Throat patches of older (ASY) males had significantly higher UV chroma and tended to be darker than throat patches of SY males. Elaboration of UV plumage ornaments in older males has been documented (Andersson and Amundsen 1997, Siefferman et al. 2005). This trend could be further clarified with reliable estimates of the exact age of individuals. Age-based indicators are simple and honest signals of quality because older males have survived longer than younger males, and tend to have increased reproductive success due to experience (Brooks and Kemp 2001). Golden-winged Warblers have a high return rate in the population studied (60% of males identified in 2005 were banded in previous years; E. A. McKinnon, unpubl. data) and often occupied the same territory. Males which return to known 'good quality' territories should be in a better position to breed earlier than younger males which may have to expend more energy fighting or searching for territories.

Older males which have better territories than younger males are probably also in better physiological condition (Marra and Holberton 1998) suggesting a proximate mechanism for age-related variation in throat patch quality. Poston et al. (2005) reported that poor nutrition has a dulling effect on the black bib of House Sparrows (*Passer domesticus*). Correlations between increased UV reflectance of melanin-based plumage and individual quality have also been documented (Siitari and Huhta 2002, Doucet et al. 2005). Golden-winged Warblers molt their throat patch in breeding areas at the end of the breeding season (Pyle 1997). Younger males with poor quality territories or less foraging experience may be in poorer nutritional condition at time of molt than older birds and, thus, have paler and less UV reflective throat patches.

Provided Golden-winged Warbler females use appearance of the throat patch to assess age and quality of a male, it is unlikely they would mate with males lacking the throat patch, such as a Blue-winged Warbler or the hybrid 'Brewster's Warbler' (*Vermivora leucobronchialis*). Leichty and Grier (2006) presented results showing that Golden-winged Warbler males whose black face pattern was

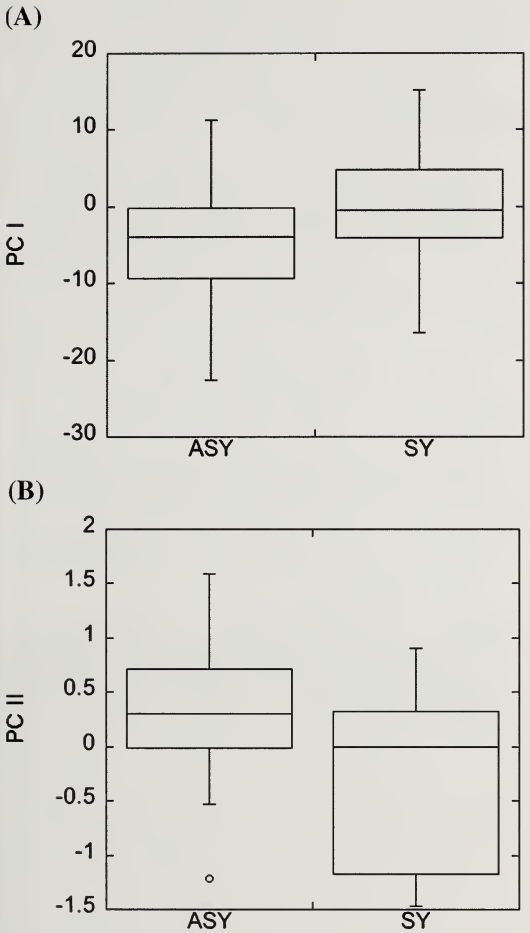


FIG. 2. Box plots showing the difference in PC I (A) and PC II (B) between ASY and SY males. Horizontal lines show 25th, 50th and 75th percentiles with lines extending to minimum and maximum values. An open circle indicates an outlier.

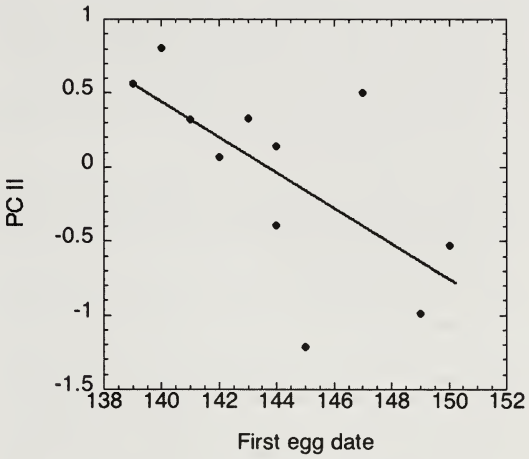


FIG. 3. Relationship between UV chroma and first egg date (ordinal date 139 represents 19 May 2005).

removed (simulating the 'Brewster's Warbler' facial pattern) were at a mating disadvantage in a pure Golden-winged Warbler population.

Leichty and Grier (2006) also found that female Golden-winged Warblers chose to mate with males which had the black throat patch. Our study found that females lay earlier when paired with males with more UV reflective throat patches. It is unclear what information, if any, the black throat patch conveys to female Blue-winged Warblers or hybrids. A study of mate preferences of Blue-winged Warblers and hybrids could further elucidate the role of plumage as a potential mechanism driving this hybridization system.

ACKNOWLEDGMENTS

Rachel Vallender is credited with the initial idea for this study and her research facilitated the fieldwork for this project. We are grateful to S. M. Doucet for help with spectrometry. K. C. Fraser provided assistance in the field and in reviewing this manuscript. S. L. Harper, Anna Yunnie, and E. A. Stancu provided field assistance. We thank the staff at the Queen's University Biological Station for field support. Laurie Smaglick-Johnson helped with field assistance and Golden-winged Warbler photographs. Robert Montgomerie provided spectrometry equipment and helpful comments. Funding was provided by the Queen's University Summer Work Experience Program, Alexander and Cora Munn Summer Research Award to EAM, and a Natural Sciences and Engineering Research Council of Canada Discovery Grant to RJR. We thank K. J. McGraw and an anonymous reviewer for helpful comments on the original manuscript.

LITERATURE CITED

Andersson, M. 1994. Sexual selection in animals. Princeton University Press, Princeton, New Jersey, USA.

Andersson, S. and T. Amundsen. 1997. Ultraviolet colour vision and ornamentation in Bluethroats. Proceedings of the Royal Society of London Series B 264:1587–1591.

Brooks, R. and D. J. Kemp. 2001. Can older males deliver the good genes? Trends in Ecology and Evolution 16:308–313.

Confer, J. L. 2006. Secondary contact and introgression of Golden-winged Warblers (*Vermivora chrysoptera*). Auk 123:958–961.

Cuthill, I. C., A. T. D. Bennett, J. C. Partridge, and E. J. Maier. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. American Naturalist 160:183–200.

Dabrowski, A., R. Fraser, J. L. Confer, and I. J. Lovette. 2005. Geographic variability in mitochondrial introgression among hybridizing populations of Golden-winged (*Vermivora chrysoptera*) and Blue-winged (*V. pinus*) warblers. Conservation Genetics 6:843–853.

Doucet, S. M., D. J. Mennill, R. Montgomerie, P. T. Boag, and L. M. Ratcliffe. 2005. Achromatic plumage reflectance predicts reproductive success in male Black-capped Chickadees. Behavioural Ecology 16:218–222.

Gill, F. 1980. Historical aspects of hybridization between Blue-winged and Golden-winged warblers. Auk 97:1–18.

Gill, F. 1997. Local cytonuclear extinction of the Golden-winged Warbler. Evolution 51:519–525.

Leichty, E. R. and J. W. Grier. 2006. Importance of facial pattern to sexual selection in Golden-winged Warbler (*Vermivora chrysoptera*). Auk 123:962–966.

Lessells, C. M. and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Marra, P. P. and R. L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia 116:284–292.

Mennill, D. J., S. M. Doucet, R. Montgomerie, and L. M. Ratcliffe. 2003. Achromatic color variation in Black-capped Chickadees, *Poecile atricapilla*: black and white signals of sex and rank. Behavioral Ecology and Sociobiology 53:350–357.

Poston, J. P., D. Hasselquist, I. R. K. Stewart, and D. F. Westneat. 2005. Dietary amino acids influence plumage traits and immune responses of male House Sparrows, *Passer domesticus*, but not as expected. Animal Behavior 70:1171–1181.

Pyle, P. 1997. Identification guide to North American birds. Part I. Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, USA.

Saetre, G. P., T. Moum, S. Bures, M. Kral, M. Adamjan, and J. Moreno. 1997. A sexually selected character displacement in flycatchers reinforces premating isolation. Nature 387:589–592.

Siefferman, L., G. E. Hill, and F. S. Dobson. 2005. Ornamental plumage coloration and condition are dependent on age in Eastern Bluebirds *Sialia sialis*. Journal of Avian Biology 36:428–435.

Siitari, H. and E. Huhta. 2002. Individual color variation and male quality in Pied Flycatchers (*Ficedula hypoleuca*): a role of ultraviolet reflectance. Behavioral Ecology 13:737–741.

Verhulst, S., J. H. van Balen, and J. M. Tinbergen. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? Ecology 76:2392–2403.

The Wilson Journal of Ornithology 120(2):371–377, 2008

FACTORS INFLUENCING FIDELITY OF HOUSE FINCHES TO A FEEDING STATION

ANDREW K. DAVIS[1,2]

ABSTRACT.—House Finches (*Carpodacus mexicanus*) in North America are a commonly-studied species, but basic aspects of their life history remain poorly understood. I banded and observed marked House Finches at a backyard feeding site in a suburban neighborhood in Atlanta, Georgia from August 2002 through July 2004 to address how age, gender, mycoplasmal conjunctivitis, and time of year affected fidelity of individual House Finches to this site. Of 386 House Finches banded, I recaptured 77 and recorded 1,210 reobservations. More than half (55%) of all birds banded were not seen again and, of those that were, almost half (44%) were seen for less than 2 months. A House Finch's age, gender, and month of capture significantly affected how many times it was subsequently encountered (recaptured or reobserved), but not the duration of time it spent at the site of banding. Young birds (HYs) were encountered more often than adults (AHYs), and females more than males. Young birds with mycoplasmal conjunctivitis were encountered less often than those without, but this was not true for adults. These data indicate high site fidelity of adults during the breeding season and low site fidelity of juveniles early in the summer that becomes higher in late summer. Most birds captured in fall were encountered for up to 3 months. These results are discussed in relation to previous studies and their implications for transmission of *Mycoplasma gallisepticum* among House Finches. *Received 1 February 2007. Accepted 8 September 2007.*

House Finches (*Carpodacus mexicanus*) in North America have become the subject of intense study in the past decade. This species has become susceptible to a newly emerged disease, mycoplasmal conjunctivitis (e.g., Hartup et al. 2001, Roberts et al. 2001a, Farmer et al. 2002, Altizer et al. 2004a, Faustino et al. 2004). This disease, caused by the bacterium *Mycoplasma gallisepticum* (MG), can cause infected House Finches to develop easily recognizable swellings around their eyes (mycoplasmal conjunctivitis) with outbreaks occurring annually during fall and winter (Altizer et al. 2004a, 2004b). House Finches are also studied because of natural variation in male plumage color and, thus, have become a focal species for study of sexual selection and male quality (e.g., Hill 1992b, 1998; Hill et al. 1999; Hill 2002). Finally, House Finches in eastern North America originated from the southwestern United States where they are non-migratory, and there is now interest in development of migratory tendencies in the expanding eastern population (Able and Belthoff 1998, Egbert and Belthoff 2003).

Ironically, despite the large number of studies involving this species, basic aspects of its' life history remain poorly understood. For example, few studies have examined movements of birds at a single site, such as at a backyard feeding station. Thus, little is known of their daily activity patterns at feeding stations, and how this changes throughout the year. What little is known comes from summaries and reports from long-term banding stations (McClure 1989, Hamilton 1992, Hilton 1994). These studies have shown that House Finches can be characterized by large-scale movements and seasonal turnover (Hamilton 1991, 1992; Hilton 1994). Previous studies contain important information, but most involved comparing rates of recapture, which may not accurately estimate fidelity to a feeding station (Hamilton 1992), and most did not examine factors affecting site fidelity, such as demographic aspects. Given that transmission of MG is likely to occur where birds gather in large numbers, such as at bird feeders, learning how feeders are used by House Finches is important. Further, since mycoplasmal conjunctivitis is a newly emerged disease, the effect of this disease on feeder use and local movements has yet to be clarified.

I report results of a 2-year study in which House Finches were trapped, uniquely banded, and reobserved at a single suburban backyard bird feeding station in an effort to elucidate the factors influencing their site fidelity.

[1] Department of Environmental Studies, Emory University, Atlanta, GA 30322, USA.

[2] Current address: Warnell School of Forestry and Natural Resources, The University of Georgia, Athens, GA 30602, USA; e-mail: akdavis@uga.edu

My specific objectives were to learn: (1) if the number of times individual House Finches captured or reobserved ('encountered') varied with time of year, age or gender, or whether or not they had conjunctivitis; and (2) if these same factors influence the duration of each individual's presence at the trap site (as measured by the time between initial capture and last encounter).

METHODS

Site Description.—The study site was the backyard of the author's house in a suburb of Atlanta, Georgia (33° 39′ N, 84° 26′ W). The yard was approximately 30 × 40 m, and contained three tube-style bird feeders on metal poles in the middle of the yard. All feeders were filled with black-oil sunflower seed, the preferred food of House Finches (Hill 1993).

Trapping and Banding.—I trapped House Finches from the beginning of August 2002 through the end of July 2004 (24 months). I conducted trapping sessions at least once a week for a minimum of 3 hrs each morning. I used a combination of mist nets (9 m long, with 30 mm mesh) placed around the feeders and two walk-in cage traps following Hill (2002). The cage traps were cylindrical and made of hardware mesh; each contained a standard bird feeder filled with sunflower seed. Two entrances in the hardware mesh near the bottom of the trap allowed birds to walk in (via a wooden perch placed outside each entrance). House Finches were readily captured by setting this trap in place of the lure feeders on trapping days.

I banded each bird upon capture with a numbered USGS metal band and three color bands in a unique color-metal band combination for later reobservation (Hill 1992a). I recorded each bird's age as either after-hatch year (AHY) or hatch-year (HY) based on skull ossification, plumage, or retrix fault bars (Pyle 1997). Similarly, I assigned gender of each bird based on the dimorphic adult plumage of the species (Hill 1993). Most HY birds were still in juvenile plumage and gender could not be assigned. I recorded the presence or absence of conjunctivitis in all birds based on outward signs of conjunctival swelling and/or ocular discharge following Altizer et al. (2004b). This same procedure was performed for all newly captured as well as recaptured birds.

Reobservations.—I watched for banded individuals at the feeding station, usually in the mornings, when activity at the feeders was high. I recorded the band combination, gender, date and time of observation, and the presence or absence of conjunctivitis whenever a banded House Finch was reobserved at or near the feeders. House Finches often visit feeders in large flocks, especially during winter (Hill 1993) and I recorded the number of other finches in the flock with the reobserved individual. Every effort was made to watch for banded individuals on most days each month.

Data Analyses.—I used the pooled trapping and reobservation data from the 24-month period for this study. I first ensured the reobservation data contained no erroneous band combinations (Milligan et al. 2003) and created two variables for testing site fidelity of House Finches. I summed all of the encounters (first capture + any subsequent recaptures or reobservations) for every bird. If the bird was not encountered after initial capture, it was assigned a '1'. I assumed this value represented the approximate frequency at which the individual used the feeding station. Second, I calculated the time in days between the first (initial capture) and last (recapture or reobservation) encounter for each individual, using only those individuals that were encountered two or more times. This value was assumed to represent the time span over which the individual visited the feeding station. I used univariate analyses of variance, using either of the above variables as dependents (after log-transformation) with age (AHY or HY), gender, conjunctivitis status (with, without), month (of initial capture), and all two-way interactions between age, gender, and conjunctivitis as independent variables. Significance was accepted when $P < 0.05$ but results were considered nearly significant when $P < 0.1$.

RESULTS

I banded 386 separate individuals over the 24-month study period (Table 1), and later made 77 recaptures and 1,210 reobservations of these individuals for a total of 1,673 encounters. Overall, 55.7% of all House Finches banded were not recaptured or reobserved after initial capture (Fig. 1A). Another 24.7%

TABLE 1. Trapping totals (new captures only) and age ratios of House Finches by month at a feeding station in Atlanta, Georgia (trapping data pooled over 2 years). House Finches could not be reliably assigned to age classes in December.

Month	% AHY	% HY	Total banded
Jan	100.0	0.0	21
Feb	100.0	0.0	16
Mar	100.0	0.0	8
Apr	100.0	0.0	10
May	16.3	83.7	43
Jun	8.3	91.7	36
Jul	6.1	93.9	49
Aug	18.2	81.8	40
Sep	33.3	66.7	62
Oct	48.1	51.9	34
Nov	38.9	61.1	35
Dec	N/A	N/A	32
Totals	34.9	65.1	386

were recorded up to five times. Combined, 80.4% of all House Finches banded were encountered between one and five times at the feeding station, and 19.6% of all House Finches were encountered more than five times. Only 6.7% of all birds were encountered 20 or more times (Fig. 1A). Examination of the time period between first and last encounter for all individuals encountered two or more times indicated 44% of the House Finches were present less than 50 days (Fig. 1B), while only 14% were encountered over a span longer than 1 year.

There were significant or nearly significant effects of age, gender, month, and an age*conjunctivitis interaction effect on number of times an individual was encountered (Table 2). There were no significant effects or significant interaction effects in the second ANOVA using time span between first and last encounter as the dependent variable. Birds captured in April, August, September, October, November, and December were all encountered more than the mean of 4.15 encounters (Fig. 2A). Birds captured in March, April, August, October, and December were subsequently encountered for longer time spans than the mean of 79.5 days (Fig. 2B). Birds captured in May, June, and July (mostly HYs; Table 1) were encountered less than 50 days. Birds captured in June were encountered only 1.5 times on average, for fewer than 50 days, but yet in June there were large flocks

TABLE 2 ANOVA examining factors influencing number of times House Finches were encountered at a feeding station in Atlanta, Georgia. The nonsignificant interaction of Gender*Conjunctivitis is not shown. Only birds of known age and gender were used in the analysis.

Variable	df	Mean square	*F*	*P*
Age	1	0.784	3.513	0.063
Gender	1	0.969	4.345	0.039
Conjunctivitis	1	0.427	1.912	0.168
Month	11	0.408	1.828	0.052
Age * Conjunctivitis	1	0.998	4.474	0.036
Gender * Age	1	0.273	1.223	0.270
Error	176	0.223		

at the feeding station (Fig. 2C). Conversely, in April, there were few House Finches observed at the feeders, but those that were captured in this month (all adults; Table 1) were later frequently encountered (~5 times) for ~5 months later (150 days).

The effects of age and gender on number of encounters per individual varied (Fig 3A). Young House Finches were encountered more often on average than adults, and females were encountered more often than males. Overall, young females were encountered most often. Birds initially captured with conjunctivitis were not subsequently encountered differently than those without (Table 2, Fig. 3B). However, there was a significant interaction of age and conjunctivitis (Table 2, Fig. 3B); adults with conjunctivitis had a slightly higher encounter rate than those without, but young birds with conjunctivitis had a lower rate than those without.

DISCUSSION

There was high seasonal turnover of House Finches at this suburban site in Georgia. High turnover rates of this species have been documented in a number of studies in eastern (Hamilton 1992) and western North America (McClure 1989). Only a small percentage of House Finches at my site frequented the feeding station over 20 times (6.7%) and for longer than 1 year (14%). These numbers indicate that only a small fraction of the House Finches observed at backyard bird feeders in suburban Atlanta, Georgia remain at individual sites year-round. Thus, most House Finches at my (and perhaps other) feeders must

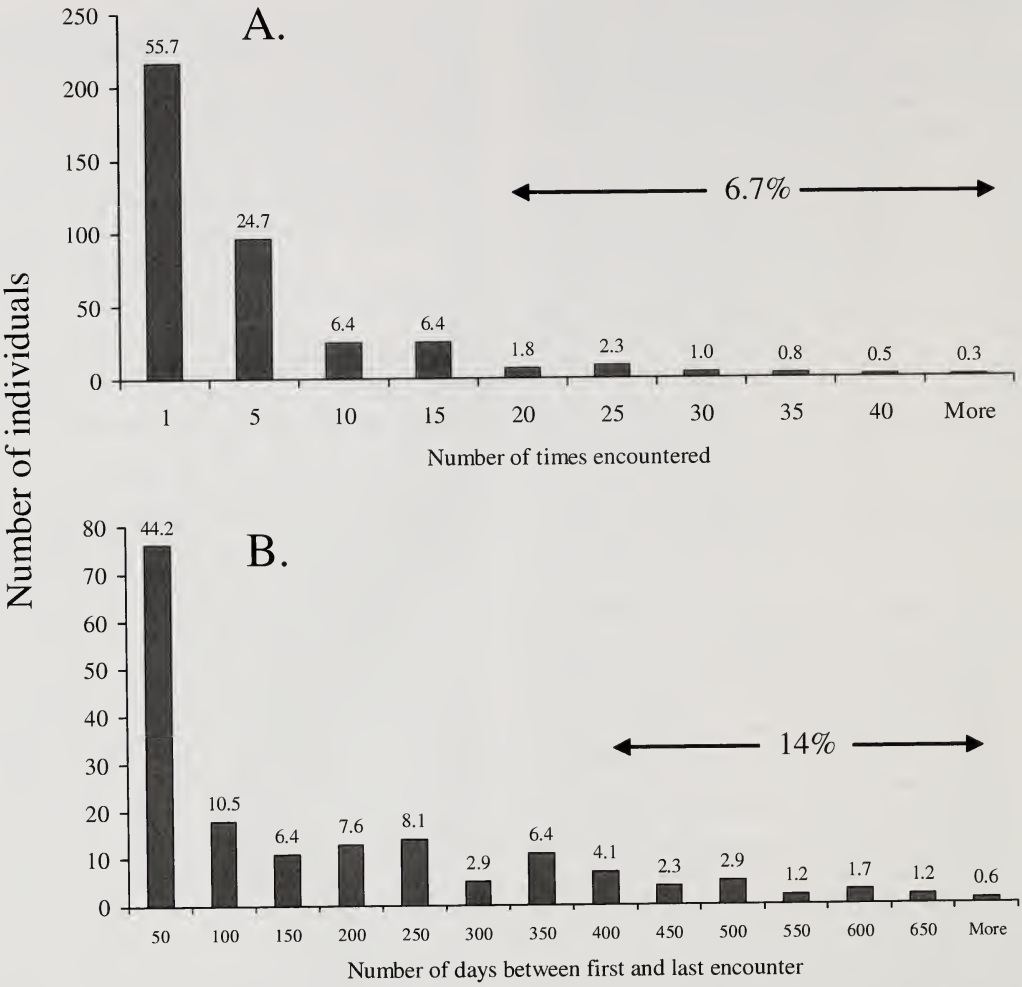


FIG. 1. A. Distribution of all House Finch encounters over 24 months. Values above bars show percentages of the total number of banded individuals (n = 386). B. Number of days between first (initial capture) and last encounters (final recapture or reobservation) of House Finches over 24 months. Only individuals with two or more encounters are included. Values above bars show percentages of the total number of banded individuals with two or more encounters (n = 172).

have been either transient individuals or young of the year that rarely remained at the site. I trapped 386 separate House Finches at this one site over the 2-year period and many new birds were trapped each month, even though the average number of birds seen at the site was <6 (Fig. 2C). Thus, it is likely that most House Finches observed at backyard feeders are infrequently the same individuals.

My data provide additional information on factors influencing feeder fidelity in House Finches. For example, there was a seasonal component to the turnover rate at this site. House Finches trapped in April, which were invariably adults (Table 1), tended to frequent the site throughout the summer, but not much longer. These probably represented adults nesting in the area throughout the summer. Flock sizes increased in May and June, which could be explained as adults and their fledglings frequenting the feeding station. Birds trapped in these months (mostly young; Table 1) were rarely seen after their initial trapping. Encounter rates increased in August and remained high through the fall. Most of the birds trapped during these months were HYs,

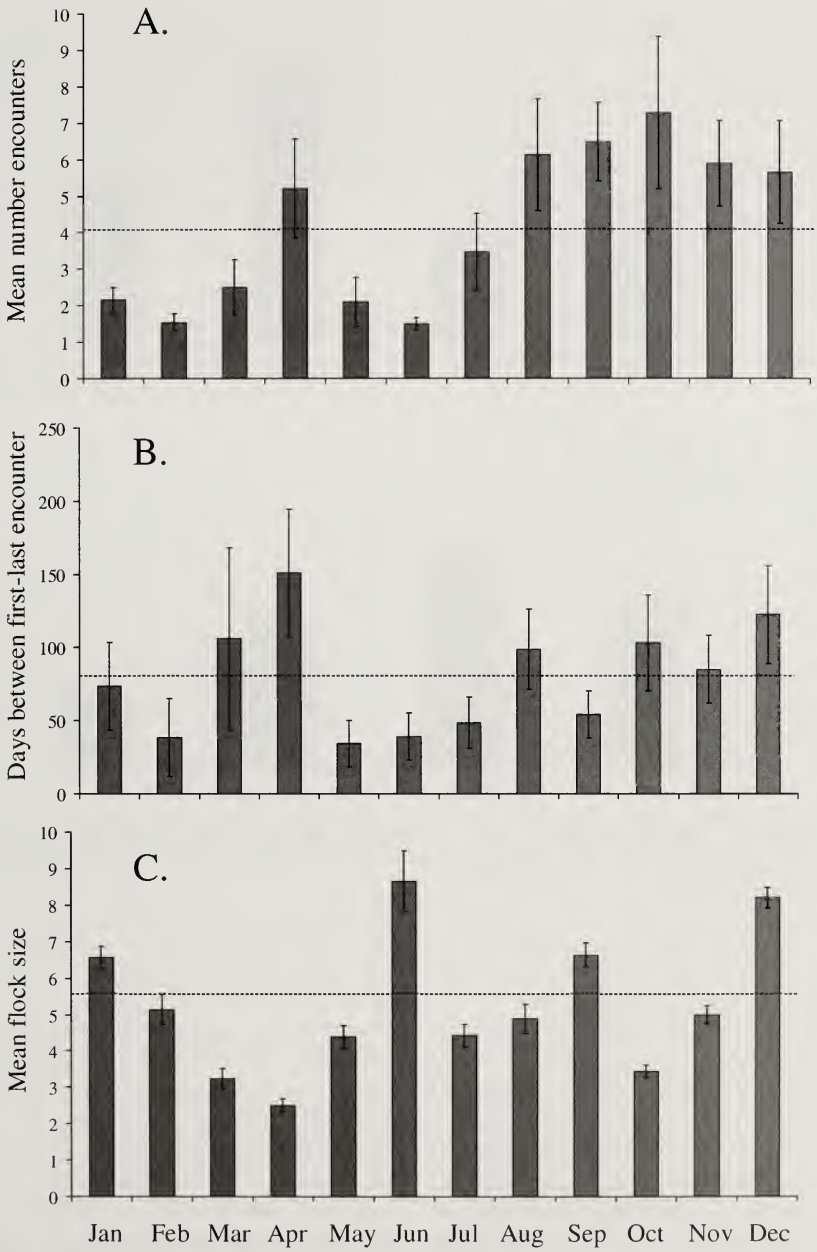


FIG. 2. A. Mean number of encounters of normal House Finches per month. B. Mean length of time between first and last encounter of normal House Finches per month. C. Monthly variation in flock sizes of House Finches observed at feeders over 24 months. Dashed lines indicate 24-month averages.

although they would have been independent of their parents and perhaps traveling in loose flocks (Hill 1993).

Seasonal turnover and fidelity to this site were characterized by high fidelity of adults during the breeding season, low fidelity of juveniles early in the summer, but becoming higher in late summer. Most birds captured in fall were encountered for up to 3 months. These might represent wintering individuals. Fidelity to this site declined in late winter and, by February, most birds captured were rarely

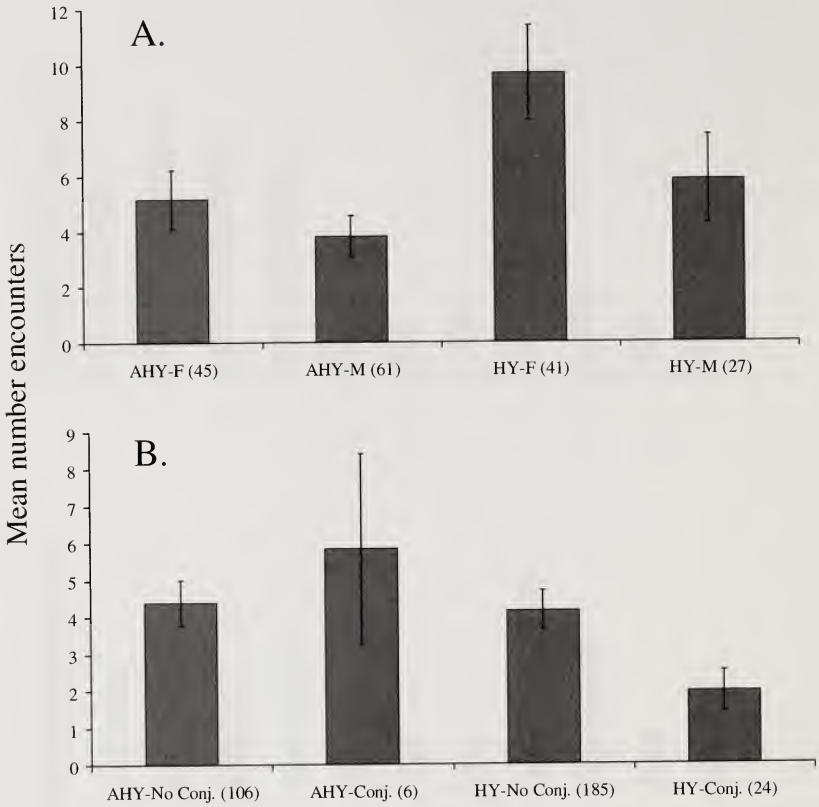


FIG. 3. A. Mean number of encounters of normal House Finches in all age and gender classes. B. Mean number of encounters of House Finches in each age/conjunctivitis category. Sample sizes for each class shown in parentheses in both charts.

seen again. Adult breeders arrived in April and remained throughout the summer.

Direct comparisons of encounter rates by age and gender classes indicated young House Finches were encountered more frequently than adults and females were encountered more than males (Fig. 3A). If the number of encounters represents relative feeder use, this result has important implications for transmission of MG. Roberts et al. (2001b) found that young birds were more likely to be clinically infected than adults. Moreover, young female House Finches were found to have conjunctivitis more than any other age and gender class (Altizer et al. 2004b). My results indicate that young females are encountered most often at a feeding station. Therefore it may be possible that younger individuals, especially females, contract this disease more often because they visit bird feeders more than other individuals, thereby coming in contact with any infected individuals or contaminated surfaces more frequently.

Also of importance to MG dynamics is the extremely high turnover of individuals I observed as 386 separate birds were trapped at a single feeding station during this 2-year study. If this feeder site typifies the use of other feeders in this geographic region, this turnover rate is likely a factor in the transmission of MG among House Finches. Moreover, increased feeder use by individuals during fall compared to other seasons (Fig. 2A) occurs in the same time period as annual outbreaks of MG in this area (Altizer et al. 2004b), thereby increasing the likelihood of transmission between individuals through contact at feeders.

The results of this study serve as an example of how the practice of bird feeding can influence the life history of a bird species. House Finches clearly have adapted to using

feeders in eastern North America (Dhondt et al. 1998) and this study shows they vary in their fidelity to these feeders by age, gender, and time of year. Increased feeder use during certain time periods or by select age/gender classes could be an important driver of the spread of *Mycoplasma gallisepticum*.

ACKNOWLEDGMENTS

Sonia Altizer provided assistance on all aspects of the project. Katherine Cook and Elizabeth Lindsey helped with trapping finches and recording data. Funding was partly provided by an NSF grant to Andre Dhondt (DEB-0094456) and by an Emory University Research grant.

LITERATURE CITED

Able, K. P. and J. R. Belthoff. 1998. Rapid 'evolution' of migratory behaviour in the introduced House Finch of eastern North America. Proceedings of the Royal Society of London Series B 265: 2063–2071.

Altizer, S. M., W. M. Hochachka, and A. A. Dhondt. 2004a. Seasonal dynamics of mycoplasmal conjunctivitis in eastern North American House Finches. Journal of Animal Ecology 73: 309–322.

Altizer, S., A. K. Davis, K. C. Cook, and J. J. Cherry. 2004b. Age, sex, and season affect the risk of mycoplasmal conjunctivitis in a southeastern House Finch population. Canadian Journal of Zoology 82:755–763.

Dhondt, A. A., D. L. Tessaglia, and R. L. Slothower. 1998. Epidemic mycoplasmal conjunctivitis in House Finches from eastern North America. Journal of Wildlife Diseases 34:265–280.

Egbert, J. R. and J. R. Belthoff. 2003. Wing shape in House Finches differs relative to migratory habit in eastern and western North America. Condor 105:825–829.

Farmer, K. L., G. E. Hill, and S. R. Roberts. 2002. Susceptibility of a naive population of House Finches to *Mycoplasma gallisepticum*. Journal of Wildlife Diseases 38:282–286.

Faustino, C., C. S. Jennelle, V. Connolly, A. K. Davis, E. C. Swarthout, A. Dhondt, and E. G. Cooch. 2004. *Mycoplasma gallisepticum* infection dynamics in a House Finch population: analysis of seasonal variation in survival and transmission rate. Journal of Animal Ecology 73:651–669.

Hamilton, T. R. 1991. Seasonal movement of House Finches in the Midwest. North American Bird Bander 16:119–122.

Hamilton, T. R. 1992. Turnover within a population of House Finches in the Midwest. North American Bird Bander 17:116–118.

Hartup, B. K., A. A. Dhondt, K. V. Sydenstricker, W. M. Hochachka, and G. V. Kollias. 2001. Host range and dynamics of mycoplasmal conjunctivitis among birds in North America. Journal of Wildlife Diseases 37:72–81.

Hill, G. E. 1992a. An inexpensive source of colored leg bands. Journal of Field Ornithology 63:408–410.

Hill, G. E. 1992b. Proximate basis of variation in carotenoid pigmentation in male House Finches. Auk 109:1–12.

Hill, G. E. 1993. House Finch (*Carpodacus mexicanus*). The birds of North America. Number 46.

Hill, G. E. 1998. Plumage redness and pigment symmetry in the House Finch. Journal of Avian Biology 29:86–92.

Hill, G. E. 2002. A red bird in a brown bag. The function and evolution of colorful plumage in the House Finch. Oxford University Press, New York, USA.

Hill, G. E., P. M. Nolan, and A. M. Stoehr. 1999. Pairing success relative to male plumage redness and pigment symmetry in the House Finch: temporal and geographic constancy. Behavioral Ecology 10:48–53.

Hilton, B. 1994. *Carpodacus* finches in South Carolina's piedmont: migration, sex ratios, site fidelity, and longevity. North American Bird Bander 19: 1–11.

McClure, H. E. 1989. Epizootic lesions of House Finches in Ventura County, California. Journal of Field Ornithology 60:421–430.

Milligan, J., A. K. Davis, and S. M. Altizer. 2003. Errors associated with using colored leg bands to identify wild birds. Journal of Field Ornithology 74:111–118.

Pyle, P. 1997. Identification guide to North American Birds. Part 1. Slate Creek Press, Bolinas, California, USA.

Roberts, S. R., P. M. Nolan, and G. E. Hill. 2001a. Characterization of *Mycoplasma gallisepticum* infection in captive House Finches (*Carpodacus mexicanus*) in 1998. Avian Diseases 45:70–75.

Roberts, S. R., P. M. Nolan, L. H. Lauerman, L.-Q. Li, and G. E. Hill. 2001b. Characterization of the mycoplasmal conjunctivitis epizootic in a House Finch population in the southeastern USA. Journal of Wildlife Diseases 37:82–88.

The Wilson Journal of Ornithology 120(2):378–383, 2008

GENDER IDENTIFICATION OF CASPIAN TERNS USING EXTERNAL MORPHOLOGY AND DISCRIMINANT FUNCTION ANALYSIS

JOSHUA T. ACKERMAN,[1,6] JOHN Y. TAKEKAWA,[2] JILL D. BLUSO,[1,3] JULIE L. YEE,[4] AND COLLIN A. EAGLES-SMITH[1,5]

ABSTRACT.—Caspian Tern (*Sterna caspia*) plumage characteristics are sexually monochromatic and gender cannot easily be distinguished in the field without extensive behavioral observations. We assessed sexual size dimorphism and developed a discriminant function to assign gender in Caspian Terns based on external morphology. We collected and measured Caspian Terns in San Francisco Bay, California, and confirmed their gender based on necropsy and genetic analysis. Of the eight morphological measurements we examined, only bill depth at the gonys and head plus bill length differed between males and females with males being larger than females. A discriminant function using both bill depth at the gonys and head plus bill length accurately assigned gender of 83% of terns for which gender was known. We improved the accuracy of our discriminant function to 90% by excluding individuals that had less than a 75% posterior probability of correctly being assigned to gender. Caspian Terns showed little sexual size dimorphism in many morphometrics, but our results indicate they can be reliably assigned to gender in the field using two morphological measurements. *Received 19 April 2007. Accepted 15 August 2007.*

Many seabird species are sexually monomorphic in plumage characteristics and gender cannot easily be assigned without extensive behavioral sampling (such as gender-specific breeding behaviors or vocalizations) (Coulter 1986, Chardine and Morris 1989, Phillips and Furness 1997, Casaux and Baroni 2000), laparotomy (Quinn 1990, Stern and Jarvis 1991) or subsequent laboratory genetic analyses (Jodice et al. 2000, Genovart et al. 2003, Quintana et al. 2003, Devlin et al. 2004, Setiawan et al. 2004). Discriminant analysis of external morphometrics is a mathematical approach that has been widely used to assign gender of seabirds, including several gulls (*Larus* spp.) (Hanners and Patton 1985, Evans et al. 1993, Mawhinney and Diamond 1999, Torlaschi et al. 2000), terns (*Sterna* spp. and *Chlidonias* spp.) (Coulter 1986, Stern and Jarvis 1991, Devlin et al. 2004, Fletcher and Hamer 2003, Bluso et al. 2006), petrels (*Fulmarus* spp., *Thalassoica* spp., *Daption* spp., and *Pagodroma* spp.) (Van Franeker and Ter Braak 1993, Weidinger and Van Franeker 1998), jaegers (*Stercorarius* spp.) (Phillips and Furness 1997), shearwaters (*Puffinus* spp.) (Genovart et al. 2003), noddy (*Anous* spp.) (Chardine and Morris 1989), shags (*Phalacrocorax* spp.) (Casaux and Baroni 2000, Quintana et al. 2003), kittiwakes (*Rissa* spp.) (Jodice et al. 2000), and Yellow-eyed Penguins (*Megadyptes antipodes*) (Setiawan et al. 2004). Discriminant analysis produces a linear combination of morphological variables that best describes the distinction between known males and females (Khattree and Naik 2000).

One prior study examined gender differences in Caspian Tern (*Sterna caspia*) morphology (Quinn 1990), but the discriminant function, which accurately assigned gender to 77% of the terns, did not incorporate head plus bill length. The distance from the back of the head to the tip of the bill (hereafter head-to-bill length) is widely used in discriminant function analyses to differentiate gender in many Laridae (Hanners and Patton 1985, Stern and Jarvis 1991, Phillips and Furness 1997, Fletcher and Hamer 2003, Devlin et al. 2004). This single measurement has distinguished gender

[1] USGS, Western Ecological Research Center, Davis Field Station, One Shields Avenue, University of California, Davis, CA 95616, USA.

[2] USGS, Western Ecological Research Center, San Francisco Bay Estuary Field Station, 505 Azuar Drive, Vallejo, CA 94592, USA.

[3] Humboldt State University, Wildlife Department, One Harpst Street, Arcata, CA 95521, USA.

[4] USGS, Western Ecological Research Center, 3020 State University Drive East, Modoc Hall, Room 3006, Sacramento, CA 95819, USA.

[5] U.S. Fish and Wildlife Service, 2800 Cottage Way, Suite W-2605, Sacramento, CA 95825, USA.

[6] Corresponding author;
e-mail: jackerman@usgs.gov

with 88-98% accuracy in some gull species (Coulson et al. 1983, Mawhinney and Diamond 1999, Jodice et al. 2000, Torlaschi et al. 2000) and linear combinations of head-to-bill length with other morphological characteristics has increased the ability to accurately assign gender of several tern species (Stern and Jarvis 1991, Fletcher and Hamer 2003, Devlin et al. 2004). Our objective was to examine sexual size dimorphism of Caspian Terns in San Francisco Bay, California, USA, and develop a discriminant function incorporating head-to-bill length and several other external measurements.

METHODS

Study Area.—San Francisco Bay, California (37.8° N, 122.3° W) is the largest estuary on the west coast of North America. Caspian Terns breed at as many as 13 different sites in San Francisco Bay (Strong et al. 2004). We sampled Caspian Terns near three breeding colonies, including a site in the North Bay (Napa River near the Carquinez Strait) and two sites in the South Bay on the Don Edwards San Francisco Bay National Wildlife Refuge (Alviso Slough and Coyote Hills Pond 2A).

Collections and Measurements.—We collected terns by shotgun under California Department of Fish and Game Scientific Collection permits (SC-801034-05 and SC-007250), U.S. Fish and Wildlife Service permit (MB120154-2), and guidelines of the USGS, Western Ecological Research Center Animal Care and Use Committee. We measured culmen length, bill depth at the gonys, head-to-bill length, tarsus length (tarsometatarsus bone), wing length (carpal joint to the end of the longest straightened primary), length of rectrices R1 and R6 (R1 was the central most rectrix on right side, R6 was the outer most rectrix on right side), and body mass for each tern. We measured tern morphology to the nearest 0.01 mm with digital calipers (Fisher Scientific, Hampton, NH, USA), except wing chord and tail measurements, which were measured to the nearest 1.0 mm with a stopped wing rule. We measured body mass to the nearest 1.0 g with a 1-kg Pesola spring scale (Pesola AG, Baar, Switzerland). One of two researchers measured terms to reduce any observer related variation in measurement error. We examined the gonads of each tern via necropsy and verified gender by genetic analysis. A drop of blood was collected from each tern for gender analysis of the chromo-helicase-DNA binding protein gene (e.g., Jodice et al. 2000, Quintana et al. 2003) at Zoogen Services Inc.®, Davis, California, USA.

Analyses.—We used analysis of variance to test differences in morphological measurements between male and female terns. We examined sexual size dimorphism (SSD) in terns by calculating the absolute value of the difference between the mean morphological measurement for females and males, and dividing this quantity by the mean value for males. We calculated the best measurements for classifying gender of Caspian Terns with a forward stepwise discriminant function analysis using PROC STEPDISC in SAS software (Morrison 1990, SAS Institute 2004). We used a criterion based on an *F*-test of Wilks' lambda (Λ) at each step of the analysis to enter the variable contributing the most or to remove the variable contributing the least discriminatory power to the model until no further variables could be entered or removed at the 0.15 significance level. We believed that a randomly captured tern was equally likely to be female or male in the absence of morphometric data; therefore, we used *a prior* probability of 50% for the likelihood of being female. We used five of the eight morphological measurements recorded in our discriminant function analysis; we excluded body mass and retrices R1 and R6, because they are more pliable and can vary over time (Kaufman 1983, Voelker 1997). We defined discriminant scores (hereafter D) as $D = -0.5(x - \mu)'\Sigma^{-1}(x - \mu)$, where $(x - \mu)'\Sigma^{-1}(x - \mu)$ represented the squared distance from a tern with measurements x to a subpopulation with mean μ and variance matrix Σ (Khattree and Naik 2000, SAS Institute 2004). We calculated discriminant scores, D_{Female} and D_{Male}, using the mean and variance of the respective genders. We classified terns into the gender for which the smallest squared distance, or the largest D score was measured. We classified terns as males if $D_{Male\text{-}Female}$, defined as $D_{Male} - D_{Female}$, was >0 and as females if $D_{Male\text{-}Female}$ was <0. We simplified discriminant scores into linear expressions without changing the effect of scoring between genders by assuming the var-

TABLE 1. Morphological measurements (mean ± SD) and sexual size dimorphism (SSD) of Caspian Terns in San Francisco Bay, California, 2006.

Measurement	Female[a]	Male[a]	$F_{1,38}$	P	SSD (%)
Bill depth (mm)	15.19 ± 0.66	16.60 ± 0.99	27.87	<0.0001	8.49
Head-to-bill (mm)	134.00 ± 3.24	137.22 ± 3.23	9.92	0.003	2.35
Tarsus (mm)	45.30 ± 2.36	46.45 ± 3.22	1.66	0.21	2.48
Culmen length (mm)	67.27 ± 2.28	68.29 ± 2.96	1.49	0.23	1.49
Wing chord (mm)	429.10 ± 6.95	430.80 ± 10.60	0.36	0.55	0.39
Tail retrix 1 (mm)	105.90 ± 4.46	109.65 ± 7.44	3.74	0.06	3.42
Tail retrix 6 (mm)	150.10 ± 8.60	151.50 ± 9.76	0.23	0.63	0.92
Tail R_6–R_1	44.20 ± 8.55	41.85 ± 6.48	0.96	0.33	5.62
Mass (g)	669.94 ± 69.85	662.02 ± 45.13	0.18	0.67	1.20

[a] Gender confirmed by necropsy and genetic analysis.

iance Σ was constant (SAS Institute 2004). We produced classification error rates with a resubstitution analysis in SAS and validated our discriminant functions using a cross-validation procedure (Lachenbruch and Mickey 1968) where each tern was classified using a function derived from the total sample excluding the tern in question (e.g., Chardine and Morris 1989, Phillips and Furness 1997). We also calculated posterior probabilities of a tern being female (Probability = $1/[1 + \exp(D_{Male\text{-}Female})]$) and plotted these values against their corresponding discriminant score. This allowed us to calculate cut-off points for discriminant scores that had a 75% probability of being a female or male.

RESULTS

We collected 40 Caspian Terns from 19 April to 15 June 2006 in San Francisco Bay. Twenty were females and 20 were males by necropsy with gender confirmed using genetic analysis. Gender assigned via necropsy was 100% in concordance with that from genetic analysis. Two of the eight morphological characteristics we measured differed between males and females with bill depth at the gonys and head-to-bill length showing the least amount of overlap between genders (Table 1). The largest proportional differences in structural measurements between males and females were also greatest in bill depth, followed by tail retrix R1 length, tarsus length, and head-to-bill length (Table 1).

Bill depth at the gonys and head-to-bill length were the best structural measurements separating male and female Caspian Terns (Wilks's $\Lambda = 0.50$: $F_{2,37} = 18.62$, $P < 0.0001$). The discriminant function with these two morphometrics correctly classified 80% of known females and 85% of known males (83% correct classification rate overall). The leave-one-out cross-validation test (Lachenbruch and Mickey 1968) also correctly classified gender of 83% of the terns. The discriminant scores were: D_{Female} = bill depth (22.1297) + head-to-bill length (12.8779) − 1,030.9089, and D_{Male} = bill depth (24.1306) + head-to-bill length (13.1927) − 1,105.3964.

Thus, Function 1 was: $D_{Male\text{-}Female}$ = bill depth (2.0008) + head-to-bill length (0.3148) − 74.4875 and we classified terns as males when $D_{Male\text{-}Female}$ was >0 and as females when $D_{Male\text{-}Female}$ was <0.

There was some overlap in morphological measurements between males and females where the probability of correctly classifying gender was reduced (Fig. 1). Terns with discriminant scores from −1.10 to 1.10 had <75% probability of being correctly assigned to gender (Fig. 2). Twenty-five percent (10 of 40) of the terns we collected were within this overlapping range. Of the 30 terns with discriminant scores outside these cutoff points, the discriminant function correctly classified 90% of the individuals (Fig. 2).

A second discriminant function using only bill depth at the gonys also was successful in classifying gender (Wilks' $\Lambda = 0.58$: $F_{1,38} = 27.87$, $P < 0.0001$). The discriminant scores for this function were: D_{Female} = bill depth (21.4758) − 163.1193, and D_{Male} = bill depth (23.4606) − 194.6647. Thus, Function 2 was: $D_{Male\text{-}Female}$ = bill depth (1.9849) − 31.5454.

This simplified discriminant function correctly classified 80% of known females and

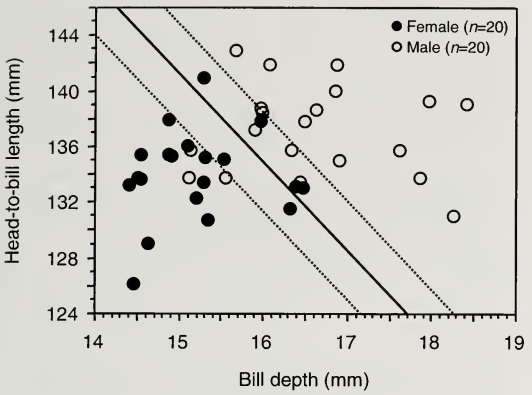


FIG. 1. Discriminant function using bill depth at the gonys and head-to-bill length to classify female (below solid line) and male (above solid line) Caspian Terns in San Francisco Bay, California. Area between the stippled lines indicates morphological overlap where the discriminant function had <75% probability of correctly classifying gender.

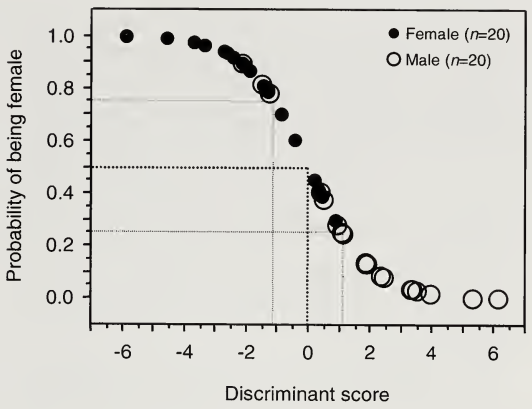


FIG. 2. Probability of being female in relation to the discriminant function scores based on bill depth and head-to-bill length of Caspian Terns in San Francisco Bay, California. All Caspian Terns with discriminant function scores <0 were classified as females and >0 as males in validation procedures. Lines indicate the cutoff points for discriminant scores of 1.10 and −1.10 if the probability of being female was set to 0.25 and 0.75, respectively.

75% of known males (78% correct classification rate overall) indicating that bill depth was the most important characteristic for differentiating gender. The cross-validation test also correctly classified 78% of the terns of known gender for Function 2.

DISCUSSION

Caspian Terns in San Francisco Bay had only slight sexual size dimorphism in most morphological characteristics we measured (Table 1). However, males were significantly larger than females in bill depth and head-to-bill length. Bill depth at the gonys was the most important morphological measurement in classifying gender of Caspian Terns and this variable alone correctly classified 78% of the terns. A discriminant function incorporating both bill depth and head-to-bill length improved our ability to accurately assign gender of Caspian Terns to 83%. Head-to-bill length and bill depth often are the most important measurements in discriminant functions for seabirds, especially larids (Hanners and Patton 1985, Van Franeker and Ter Braak 1993, Phillips and Furness 1997, Mawhinney and Diamond 1999, Torlaschi et al. 2000, Genovart et al. 2003, Devlin et al. 2004). Our accuracy is slightly better than that reported by Quinn (1990) who developed an earlier discriminant function for Caspian Terns in Texas. He found that 77% of Caspian Terns could be accurately assigned to gender using a function incorporating several morphological measurements including bill depth and culmen length, but not head-to-bill length. Quinn (1990) found that head-to-bill length was significantly larger in male than female Caspian Terns, but this morphometric was not incorporated into his discriminant function.

Our accuracy of 83% for Caspian Terns is comparable to other studies of Laridae. Our discriminant function based on bill depth and head-to-bill length was 5-11% more accurate than functions of multiple morphological characteristics developed for several other tern species (Coulter 1986, Quinn 1990, Stern and Jarvis 1991, Fletcher and Hamer 2003, Devlin et al. 2004), but 3% lower than the function we developed for Forster's Terns (*Sterna forsteri*) (Bluso et al. 2006). For example, using model validation procedures, 73 and 74% of Arctic Terns (*S. paradisaea*) (Fletcher and Hamer 2003, Devlin et al. 2004), 72 and 78% of Common Terns (*S. hirundo*) (Coulter 1986, Fletcher and Hamer 2003), 78% of Black Terns (*Chlidonias niger*) (Stern and Jarvis 1991), and 86% of Forster's Terns (Bluso et al. 2006) were correctly classified as male or female.

Discriminant functions that have been developed for gulls are, in general, more accu-

rate than functions derived for terns. Using multiple morphological measurements, discriminant functions for gulls have accurately classified gender of 90-99% of individuals (Mills 1971, Hanners and Patton 1985, Evans et al. 1993, Mawhinney and Diamond 1999, Torlaschi et al. 2000). The difference in classification rates between Caspian Terns and other Laridae suggests that Caspian Terns exhibit greater sexual size dimorphism than several other terns, but are not as dimorphic as most gull species.

We observed some overlap in morphological measurements between male and female Caspian Terns where the probability of correctly classifying an individual was reduced (Fig. 1). Posterior probabilities can be calculated and individuals with probabilities <75% can be excluded to increase the probability of correctly classifying a tern as male or female. Ten of 40 Caspian Terns we collected were within this range (Fig. 2). Our accuracy increased to 90% after excluding these terns. We caution that excluding terns within this overlapping size range could introduce bias into some studies because researchers would necessarily be classifying only the largest males and smallest females.

ACKNOWLEDGMENTS

This research was funded by the CALFED Ecosystem Restoration Program (grant # ERP-02D-C12) with additional support from the USGS, Western Ecological Research Center. We thank Sarah Stoner-Duncan, Terry Adelsbach, John Henderson, Mark Ricca, Cathy Johnson, Carolyn Marn, Angela Rex, Joe Northrup, Lani Stinson, Maliheh Nakhai, Stacy Moskal, Eli French, Kristen Dybala, Brooke Hill, and Susan Wainwright-De La Cruz for field assistance. We also thank Clyde Morris, Joy Albertson, Mendel Stewart, Joelle Buffa, Marge Kolar, Eric Mruz, John Krause, Tom Huffman, Larry Wyckoff, Carl Wilcox, Karen Taylor, Rick Morat, Lew Allen, Carol Atkins, Donna Podger, Nicole Athearn, Can Duck Club, California Department of Fish and Game, and staff at the Don Edwards San Francisco Bay National Wildlife Refuge (Special Use Permit 11640-2006-006) for logistical support, technical assistance, and access. Early versions of the manuscript were improved from comments by Cheryl Strong and two anonymous reviewers. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Bluso, J. D., J. T. Ackerman, J. Y. Takekawa, and J. L. Yee. 2006. Using morphological measurements to sex Forster's Terns. Waterbirds 29:511–516.

Casaux, R. and A. Baroni. 2000. Sexual size dimorphism in the Antarctic Shag. Waterbirds 23:489–493.

Chardine, J. W. and R. D. Morris. 1989. Sexual size dimorphism and assortative mating in the Brown Noddy. Condor 91:868–874.

Coulson, J. C., C. S. Thomas, J. E. L. Bufferfield, N. Duncan, P. Monaghan, and C. Shedden. 1983. The use of head and bill length to sex live gulls Laridae. Ibis 125:549–557.

Coulter, M. C. 1986. Assortative mating and sexual dimorphism in the Common Tern. Wilson Bulletin 98:93–100.

Devlin, C. M., A. W. Diamond, and G. W. Saunders. 2004. Sexing Arctic Terns in the field and laboratory. Waterbirds 27:314–320.

Evans, D. R., E. M. Hoopes, and C. R. Griffin. 1993. Discriminating the sex of Laughing Gulls by linear measurements. Journal of Field Ornithology 64:472–476.

Fletcher, K. L. and K. C. Hamer. 2003. Sexing terns using biometrics: the advantage of within-pair comparisons. Bird Study 50:78–83.

Genovart, M., M. McMinn, and D. Bowler. 2003. A discriminant function for predicting sex in Balearic Shearwater. Waterbirds 26:72–76.

Hanners, L. A. and S. R. Patton. 1985. Sexing Laughing Gulls using external measurements and discriminant analysis. Journal of Field Ornithology 56:158–164.

Jodice, P. G. R., R. B. Lanctot, V. A. Gill, D. D. Roby, and S. A. Hatch. 2000. Sexing adult Black-legged Kittiwakes by DNA, behavior, and morphology. Waterbirds 23:405–415.

Kaufman, K. E. 1983. Tail moult of Forster's Tern. British Birds 76:357.

Khattree, R. and D. N. Naik. 2000. Multivariate data reduction and discrimination with SAS Software. SAS Institute Inc., Cary, North Carolina, USA.

Lachenbruch, P. A. and M. R. Mickey. 1968. Estimation of error rates in discriminant analysis. Technometrics 10:1–11.

Mawhinney, K. and T. Diamond. 1999. Sex determination of Great Black-backed Gulls using morphometric characters. Journal of Field Ornithology 70:206–210.

Mills, J. A. 1971. Sexing Red-billed Gulls from standard measurements. Journal of Marine and Freshwater Research 5:326–328.

Morrison, D. F. 1990. Multivariate statistical methods, Third Edition. McGraw Hill Inc., New York, USA.

Phillips, R. A. and R. W. Furness. 1997. Predicting the sex of Parasitic Jaegers by discriminant analysis. Waterbirds 20:14–23.

Quinn, J. S. 1990. Sexual size dimorphism and parental care patterns in a monomorphic and dimorphic larid. Auk 107:260–274.

Quintana, F., G. Somoza, M. Uhart, C. Cassara, P. Gandini, and E. Frere. 2003. Sex determination of adult Rock Shags by molecular sexing and

morphometric parameters. Journal of Field Ornithology 74:370–375.

SAS Institute Inc. 2004. SAS OnlineDoc®. Version 9.1.2. SAS Software, SAS Institute Inc., Cary, North Carolina, USA. http://v8doc.sas.com/sashtml/ (accessed 28 September 2006).

Setiawan, A. N., J. T. Darby, and D. M. Lambert. 2004. The use of morphometric measurements to sex Yellow-eyed Penguins. Waterbirds 27:96–101.

Stern, M. A. and R. L. Jarvis. 1991. Sexual dimorphism and assortative mating in Black Terns. Wilson Bulletin 103:266–271.

Strong, C. M., L. B. Spear, T. P. Ryan, and R. E. Dakin. 2004. Forster's Tern, Caspian Tern, and California Gull colonies in the San Francisco Bay: habitat use, population sizes and trends, 1982–2003. Waterbirds 27:411–423.

Torlaschi, C., P. Gandini, E. Frere, and R. M. Peck. 2000. Predicting the sex of Kelp Gulls by external measurements. Waterbirds 23:518–520.

Van Franeker, J. A. and C. J. F. Ter Braak. 1993. A generalized discriminant for sexing fulmarine petrels from external measurements. Auk 110: 492–502.

Voelker, G. 1997. The molt cycle of the Arctic Tern, with comments on aging criteria. Journal of Field Ornithology 68:400–412.

Weidinger, K. and J. A. Van Franeker. 1998. Applicability of external measurements to sexing of the Cape Petrel *Daption capense* at within-pair, within-population and between-population scales. London Journal of Zoology 245:473–482.

The Wilson Journal of Ornithology 120(2):384–389, 2008

EFFECTS OF TRAFFIC NOISE ON AUDITORY SURVEYS OF URBAN WHITE-WINGED DOVES

JEFFREY B. BREEDEN,[1,4] FIDEL HERNÁNDEZ,[1,5] RALPH L. BINGHAM,[1] NOVA J. SILVY,[2] AND GARY L. WAGGERMAN[3]

ABSTRACT.—We investigated the effects of urban noise on auditory surveys of White-winged Doves (*Zenaida asiatica*) in two major cities in Texas. We conducted auditory point counts throughout the morning in San Antonio (n = 6) and Austin (n = 10) during week days (when traffic noise is higher) and weekends. We categorized survey points as near or far from roads (<0.8 and >0.8 km, respectively) for comparison. We documented no difference in density estimates in Austin between week days (46 ± 10 pairs/ha) and weekends (52 ± 10 pairs/ha; P = 0.23); however, weekend estimates were consistently higher throughout the morning. Weekend density estimates in San Antonio were higher after 0620 hrs (P < 0.04), the time coinciding with beginning of the morning commute during week days in this city. We documented that weekend estimates (45 ± 5 pairs/ha) were higher than week day estimates (33 ± 5 pairs/ha) for points near roads (within 0.8 km; P = 0.02) but not for points far from roads (P = 0.16). Our results indicate that traffic noise can bias auditory surveys. Survey methods that account for probability of detection should be used to correct for potential noise bias. *Received 24 May 2007. Accepted 20 September 2007.*

Auditory point-count indices are commonly used to estimate abundance of avian populations. The assumption is the number of birds heard calling provides an accurate index to abundance (Sisson 1968, Keppie et al. 1970); however, the validity of indices recently has been questioned (Anderson 2001, Thompson 2002). Factors such as observer variability, habitat variables, and weather can affect detection of calling birds potentially biasing surveys (LaPerriere and Haugen 1972, Shields 1977, Baskett et al. 1978). Human-induced disturbances such as traffic noise can also bias auditory surveys. Assessing potential bias in auditory surveys due to traffic noise is important considering the need to accurately assess the status of wildlife populations and the likelihood that traffic noise will increase with an expanding human population.

Little research exists regarding the potential influence of traffic noise on auditory survey methods in urban areas. Due to their calling frequency and urban populations, the White-Winged Dove (*Zenaida asiatica*) is a good species to study to gain insight into the effects of noise disturbance on auditory counts. West (1993) evaluated the accuracy of the White-winged Dove call-count index in San Antonio, Texas, but did not assess the effects of noise. Emlen and DeJong (1981) suggested that surveys should be conducted only when background-noise level was within acceptable limits with correction factors applied for noise bias, if necessary. Dawson (1981), however, reported that environmental noise had little effect on number of Grey Gerygone (*Gerygone igata*) counted in New Zealand forests, but suggested that it could act through effects on observers and birds.

Historically, White-winged Doves occurred in rural environments in southern Texas and northern Mexico during the breeding season. The species has been expanding its distribution northward and increasing in density in Texas, and has become common in urban areas outside its historic range (George et al. 1994, Waggerman 2001). Urban surveys were initiated by the Texas Parks and Wildlife Department (TPWD) in San Antonio and Austin during the late 1980s in response to the range expansion. TPWD biologists assumed that traffic volume, and thus traffic noise, was greater during early morning on week days, because of commuter traffic, rather than on

[1] Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA.

[2] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 78840, USA.

[3] Texas Parks and Wildlife Department, 1221 Ranch Road 12, San Marcos, TX 78666, USA.

[4] Current address: Department of Animal Sciences, Box T-0070, Tarleton State University, Stephenville, TX 76402, USA.

[5] Corresponding author;
e-mail: fidel.hernandez@tamuk.edu

weekends when designing these urban surveys. Protocol therefore mandated that urban surveys be conducted only during early morning on weekends in an effort to reduce potential noise bias. However, this constrained sampling period allowed little time to complete urban surveys. Thus, more effort was required by biologists and volunteers to complete urban surveys within the specified time period making the process less efficient.

Additional urban areas need to be monitored in the future with the continuing northward range expansion of White-winged Doves. Thus, knowledge of the potential impacts of urban noise on auditory counts is needed. The objective of this study was to examine if abundance estimates obtained through auditory counts for urban populations of White-winged Doves varied between time periods (i.e., week day vs. weekend) when traffic noise differed.

METHODS

We selected a sample of survey points from the total used in the annual survey of White-winged Doves from Austin (n = 10 selected; n = 122–204 total) and San Antonio (n = 6 selected; n = 219–241 total), Texas as described by Breeden et al. (2004). Research has indicated that calling frequency of some columbids may be more variable at lower densities (Cohen et al. 1960, Keppie et al. 1970, Viers 1970). Thus, we chose points at which previous surveys estimated dove densities were >25 pairs/ha to reduce potential bias associated with lower densities. We conducted auditory counts during 15 May–15 June 2004 following Rappole and Waggerman (1986). We calculated density estimates (pairs/ha) at each survey point based on observed calling intensity following Uzzell and Kiel (1950) and Sepúlveda et al. 2006. We surveyed each point twice: once during a week day (Monday–Friday) and once during a weekend (Saturday–Sunday) to examine if survey period influenced auditory counts. Observers conducted auditory counts once per 20-min interval at each survey point throughout the morning during 0540–1100 hrs CST. We chose this time period because peak White-winged dove calling occurs during morning hours (Sepúlveda et al. 2006). Each observer sampled two survey points during a morning.

We compared points near (<0.8 km) and far (>0.8 km) from high-traffic roads (i.e., >4 traffic lanes) to further examine the possible effects of traffic noise on calling intensity. We used 0.8 km as a threshold value for traffic noise because, based on our experience, traffic noise affected observers' hearing ability within this distance.

Statistical Analysis.—We used a repeated measures ANOVA model to test for differences between week day and weekend density estimates in Austin and San Antonio using SAS (SAS Institute 2001). We used the same procedure to test for differences between week day and weekend density estimates for points near and far from roads. Counts for a particular time interval occasionally were not recorded because the observer was unable to sample a point during the chosen time interval due to traffic delays. The corresponding observation in the same time interval of the comparison trial was omitted if a call count was not recorded for a particular time interval. We present results as means ± SE and report density estimates as pairs/ha. We use the term "period" to refer to survey period on week days or weekends.

RESULTS

We did not find an interaction between period and time of day in Austin ($F_{15,270}$ = 0.72, P = 0.77) and therefore pooled across time of day (Fig. 1). There was no difference in density estimates between week days (46 ± 10 pairs/ha) and weekends (52 ± 10 pairs/ha; $F_{1,9}$ = 1.63, P = 0.23). However, weekend estimates were consistently higher throughout the morning (Fig. 1). We did find an interaction for San Antonio between period and time of day ($F_{15,132}$ = 2.49, P < 0.01). Thus, we compared week day and weekend density estimates in San Antonio for each 20-min interval between 0540–1100 hrs. There was no difference in density estimates between week day and weekend estimates before 0620 hrs (P > 0.20) (Fig. 1) after which weekend estimates were higher (Table 1, P < 0.04).

We did not find an interaction between period and time of day for points near roads ($F_{15,249}$ = 1.18, P = 0.29) or for points far from roads ($F_{15,134}$ = 0.45, P = 0.96). Weekend estimates (45 ± 5 pairs/ha) were higher than week day estimates (33 ± 5 pairs/ha) for

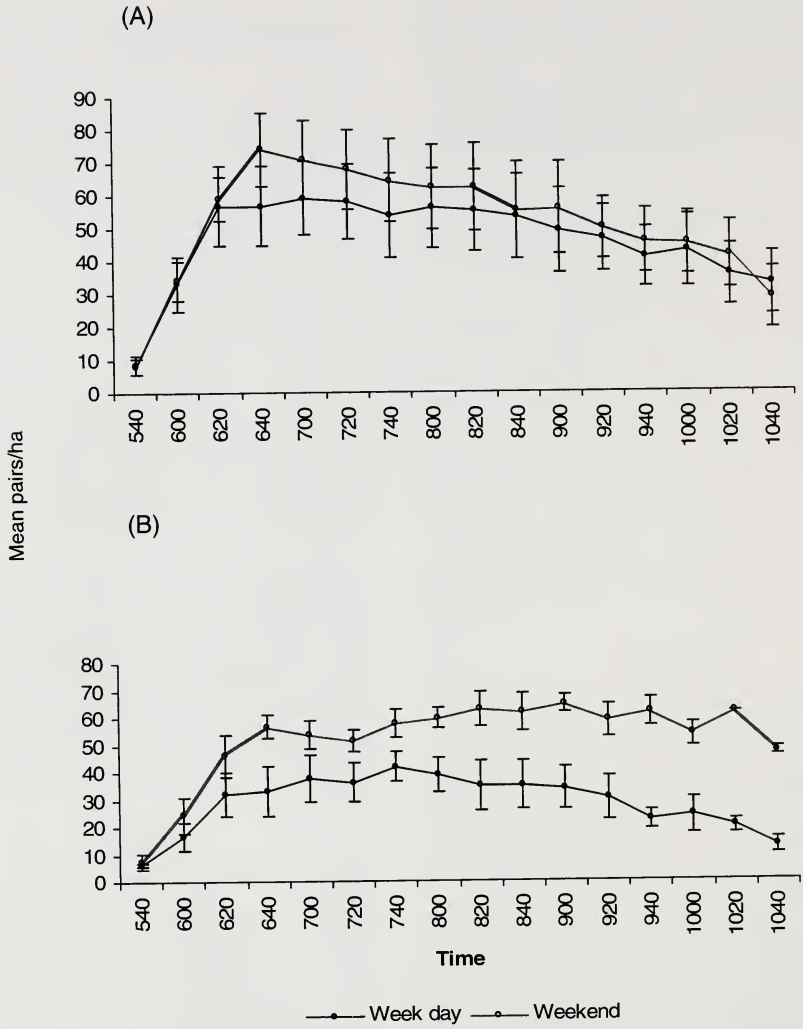


FIG. 1. White-winged Dove density estimates (mean ± SE) during week day- and weekend-morning auditory counts in (A) Austin (n = 10 survey points) and (B) San Antonio, Texas (n = 6 survey points), May–June 2004.

points near roads ($F_{1,9}$ = 7.46, P = 0.02) (Fig. 2). However, we did not find any difference between week day (52 ± 16 pairs/ha) and weekend (57 ± 16 pairs/ha) density estimates for points far from roads ($F_{1,5}$ = 2.76, P = 0.16) (Fig. 2).

DISCUSSION

We obtained higher White-winged Dove density estimates during all weekend surveys compared to week day surveys. We documented statistically greater White-winged Dove densities on weekends in San Antonio only after 0640 hrs, the time coinciding with the beginning of the morning commute during week days in this city. Differences between week day and weekend estimates were particularly evident when data were analyzed by distance from roads. We observed differences in density estimates between week day and weekend surveys at points that were within 0.8 km of roads but not at points greater than 0.8 km. Thus, our data suggest there is noise-induced bias for auditory surveys conducted in an urban environment.

Noise may affect auditory surveys through

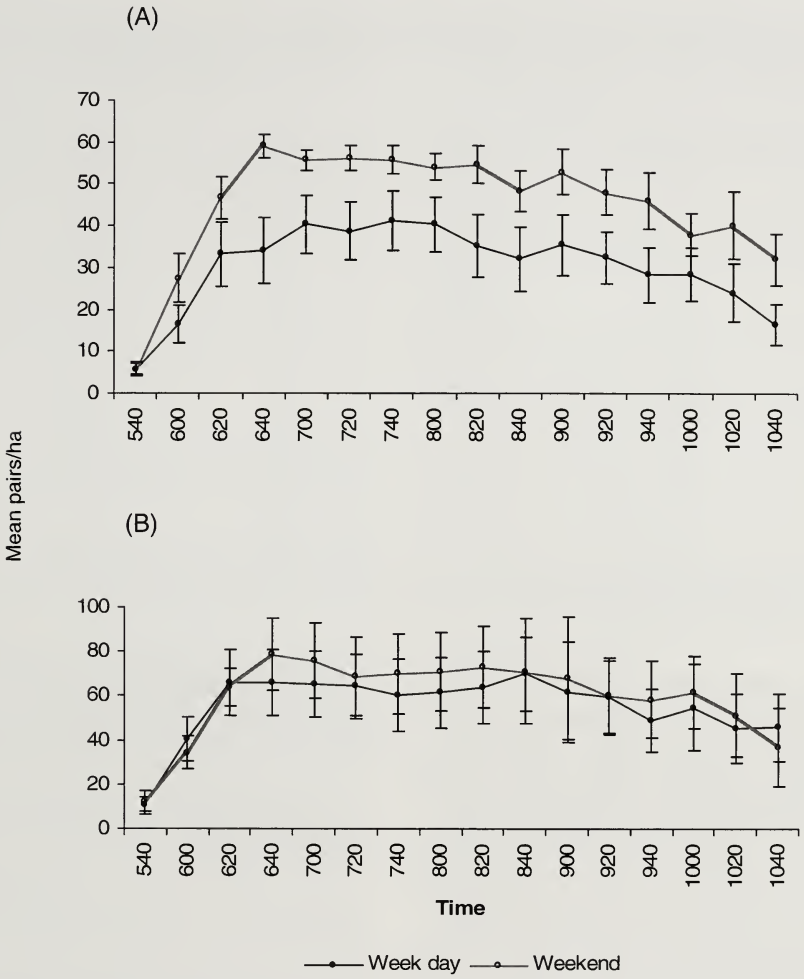


FIG. 2. White-winged Dove density estimates (mean ± SE) during week day- and weekend-morning auditory counts at (A) survey points (n = 9) within 0.8 km of a high-traffic road of four lanes or greater, and (B) survey points (n = 7) >0.8 km of a high traffic road of four lanes or greater, San Antonio and Austin, Texas, May–June 2004.

several mechanisms including masking effects, altered behavior, and density changes. Several studies have documented that increased noise often causes birds to alter their calling behavior (Slabbekoorn and Smith 2002, Slabbekoorn and Peet 2003, Brumm 2004). For example, Brumm (2004) documented that male Common Nightingales (*Luscinia megarhynchos*) in noisier territories sang at a higher volume than birds at less noisy locations to increase detection of song by potential mates. Slabbekoorn and Peet (2003) reported that Great Tits (*Parus major*) also adjusted to high human noise disturbance by singing at a higher mean frequency. Slabbekoorn and Smith (2002) reported similar adjustments by Little Greenbuls (*Andropadus virens*), where males living in quiet rain forests sang at low-frequency notes that were not used by those inhabiting ecotone forests where high levels of environmental noise masked low-pitched notes.

Noise also may result in changes in actual bird density. Reijnen et al. (1995, 1997) reported that stress due to traffic noise was the most important factor in reducing bird activity and density along roadways. Forman et al. (2002) documented that bird presence and breeding were reduced up to 1,200 m from a busy road. Reijnen and Foppen (1994) docu-

TABLE 1. White-winged Dove density estimates during week day and weekend auditory counts conducted during morning (0540–1100 hrs) in San Antonio, Texas (n = 6 points), May–June 2004.

Time	$\bar{X} \pm SE$[a]		df	t-value	P-value
	Week day	Weekend			
0540–0559	12 ± 7	9 ± 7	54.7	0.45	0.653
0600–0619	17 ± 6	24 ± 6	34.9	−1.23	0.227
0620–0639	32 ± 6	46 ± 6	34.9	−2.20	0.035
0640–0659	33 ± 6	57 ± 6	34.9	−3.69	0.001
0700–0719	38 ± 6	54 ± 6	34.9	−2.46	0.019
0720–0739	36 ± 6	52 ± 6	34.9	−2.39	0.022
0740–0759	42 ± 6	58 ± 6	34.9	−2.46	0.019
0800–0819	39 ± 6	60 ± 6	34.9	−3.30	0.002
0820–0839	35 ± 6	63 ± 6	34.9	−4.40	0.000
0840–0859	35 ± 6	59 ± 7	43.1	−3.60	0.001
0900–0919	40 ± 7	66 ± 7	54.7	−3.49	0.001
0920–0939	36 ± 7	60 ± 7	54.7	−3.16	0.003
0940–0959	28 ± 7	63 ± 7	54.7	−4.64	0.000
1000–1019	27 ± 8	52 ± 8	71.6	−2.93	0.005
1020–1039	22 ± 9	59 ± 9	94.0	−3.75	0.000
1040–1100	18 ± 7	48 ± 7	54.7	−3.98	0.000

[a] Least squares means shown for density estimates (pairs/ha).

mented that male Willow Warblers (*Phylloscopus trochilus*) close to highways experienced difficulties in attracting or keeping a female, possibly because traffic noise along roadways could distort their breeding song.

Our study and prior research suggests that urban surveys should consider the effect of urban noise on auditory counts to minimize potential bias. Abundance estimators that account for differences in detection such as distance sampling (Buckland et al. 2001) may be an effective alternative to reduce error associated with decreased detection resulting from traffic noise disturbance (Rosenstock et al. 2002, Anderson 2003, Breeden 2005).

ACKNOWLEDGMENTS

We thank Texas Parks and Wildlife Department summer interns, Susanne Contreras and Steve Cortez for conducting these surveys. D. G. Hewitt, M. J. Peterson, J. A. Roberson, and 2 anonymous reviewers provided helpful comments on an early version of this manuscript. Funding was provided by the Texas Parks and Wildlife Department's White-winged Dove Stamp Fund. This paper is Caesar Kleberg Wildlife Research Institute manuscript 05-121.

LITERATURE CITED

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. Wildlife Society Bulletin 31:288–291.

Baskett, T. S., M. J. Armbruster, and M. W. Sayre. 1978. Biological perspectives for the Mourning Dove call-count survey. Transactions of the North American Wildlife and Natural Resources Conference 43:163–180.

Breeden, J. B. 2005. An assessment of survey methods for White-winged Dove populations in urban environments. Dissertation. Texas A&M University-Kingsville, Kingsville, USA.

Breeden, J. B., F. Hernandez, N. J. Silvy, R. L. Bingham, and G. L. Waggerman. 2004. An evaluation of sampling methods for White-winged Dove surveys in urban areas. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 58:274–281.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73:434–440.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, USA.

Cohen, A., H. S. Peters, and L. E. Foote. 1960. Calling behavior of Mourning Doves in two midwest life zones. Journal of Wildlife Management 24: 203–212.

Dawson, D. G. 1981. Counting birds for a relative measure (index) of density. Studies in Avian Biology 6:12–16.

Emlen, J. T. and M. J. DeJong. 1981. The application of song detection threshold distance to census operations. Studies in Avian Biology 6:346–352.

Forman, R. T. T., B. Reineking, and A. M. Hersperger. 2002. Road traffic and nearby grassland bird patterns in a suburbanizing landscape. Environmental Management 29:782–800.

George, R. R., R. E. Tomlinson, R. W. Engel-Wilson, G. L. Waggerman, and A. G. Spratt. 1994. White-winged Dove. Pages 29–52 *in* Migratory shore and upland game bird management in North America (T. C. Tacha and C. E. Braun, Editors). International Association of Fish and Wildlife Agencies, Washington D.C., USA.

Keppie, D. M., H. M. Wight, and W. S. Overton. 1970. A proposed Band-tailed Pigeon census—a management need. Transactions of the North American Wildlife and Natural Resources Conferences 35:157–171.

LaPerriere, A. J. and A. O. Haugen. 1972. Some factors influencing calling activity of wild Mourning Doves. Journal of Wildlife Management 36: 1193–1198.

Rappole, J. H. and G. L. Waggerman. 1986. Calling males as an index of density for breeding White-winged Doves. Wildlife Society Bulletin 14:151–155.

Reijnen, R. and R. Foppen. 1994. The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for Willow Warblers (*Phylloscopus trochilus*) breeding close to a highway. Journal of Applied Ecology 31:85–94.

Reijnen, R., R. Foppen, and G. Veenbass. 1997. Disturbance by traffic of breeding birds: evaluation of the effect and considerations in planning and managing road corridors. Biodiversity and Conservation 6:567–581.

Reijnen, R., R. Foppen, C. T. Braak, and J. Thissen. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. Journal of Applied Ecology 32:187–202.

Rosenstock, S. S., D. R. Anderson, K. M. Giesen, T. Leukering, and M. F. Carter. 2002. Landbird counting techniques: current practices and an alternative. Auk 119:46–53.

SAS Institute. 2001. SAS software release 8.2. SAS Institute Inc., Cary, North Carolina, USA.

Sepúlveda, M., F. Hernández, D. G. Hewitt, W. P. Kuvlesky Jr., G. Waggerman, and R. L. Bingham. 2006. An evaluation of auditory counts for estimating breeding populations of White-winged Doves. Journal of Wildlife Management 70:1393–1402.

Shields, W. H. 1977. The effect of time of day on avian census results. Auk 94:380–383.

Sisson, L. H. 1968. Calling behavior of Band-tailed Pigeons in reference to a census technique. Thesis. Oregon State University, Corvallis, USA.

Slabbekoorn, H. and M. Peet. 2003. Birds sing at a higher pitch in urban noise. Nature 424:267.

Slabbekoorn, H. and T. B. Smith. 2002. Habitat-dependent song divergence in the Little Greenbul: an analysis of environmental selection pressures on acoustic signals. Evolution 56:1849–1858.

Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 119:18–25.

Uzzell, P. B. and W. H. Kiel Jr. 1950. Unpublished progress report. Texas Parks and Wildlife Department, Austin, USA.

Viers Jr., C. 1970. The relationship of calling behavior of White-winged Doves to population and production in southern Arizona. Dissertation. University of Arizona, Tucson, USA.

Waggerman, G. L. 2001. White-winged Dove density, distribution, movement, and harvest. Performance Report. Federal Aid Project W-128-R, Job 9. Texas Parks and Wildlife Department, Austin, USA.

West, L. M. 1993. Ecology of breeding White-winged Doves in the San Antonio metropolitan area. Thesis. Texas Tech University, Lubbock, USA.

Short Communications

The Wilson Journal of Ornithology 120(2):390–392, 2008

Specimen Shrinkage in Cinnamon Teal

Robert E. Wilson[1,2] and Kevin G. McCracken[1]

ABSTRACT.—Body size measurements from freshly collected birds and dried museum specimens were used to evaluate specimen shrinkage in Cinnamon Teal (*Anas cyanoptera*). Six of seven body measurements of female Cinnamon Teal differed significantly after specimen drying, whereas five of seven male body measurements differed. The largest amount of shrinkage was in bill height, bill width, and tarsus length. Bill length at nares showed no significant shrinkage suggesting it is a more conservative measurement than exposed culmen and, therefore, a more reliable method for accurately measuring bill length. Correction values for body size measurements are reported for future waterfowl studies combining measurements of both live birds and museum specimens. *Received 1 March 2007. Accepted 6 September 2007.*

Specimen shrinkage during the process of drying is common. Shrinkage can cause analytical problems if not properly corrected in studies involving live or freshly killed birds and museum specimens (e.g., Winker 1996). Correction for shrinkage is needed before applying to live birds when developing classification criteria for gender, subspecies, or species based on morphological features from museum specimens (Greenwood 1979, Jenni and Winkler 1989, Winker 1993). For example, Mueller (1990) reported that a shrinkage value of 1.72% would comprise 34% of wing length differences between male and female Northern Saw-whet Owls (*Aegolius acadicus*). In addition, the amount of shrinkage varies among body parts and species (Winker 1993).

Shrinkage values from one taxon may have limited use outside that particular taxon or similar morphological species because of the morphological diversity of birds and variety of preparation techniques (Jenni and Winkler 1989, Winker 1993). Specimen shrinkage in waterfowl has yet to be investigated. This paper reports shrinkage values for Cinnamon Teal (*Anas cyanoptera*), which may be used to develop correction values for similar size (~350–550 g) waterfowl.

METHODS

Cinnamon Teal are widespread throughout the Western Hemisphere and five subspecies currently are recognized (Snyder and Lumsden 1951, Delacour 1956, AOU 1957, Johnsgard 1978, Gammonley 1996). The three most widespread subspecies of Cinnamon Teal (*A. c. cyanoptera*, *A. c. orinomus*, and *A. c. septentrionalium*; 26 females, 80 males) were collected in Argentina (2003), Peru (2002), and western United States (2002–2003) as part of a larger population genetic and morphological study. Even though subspecies are distinct in overall body size, there is overlap in measurements among subspecies (R. E. Wilson, unpubl. data). Therefore, different subspecies were pooled for each gender to ascertain the extent of shrinkage for each measurement.

Seven body measurements were recorded for each bird (± 0.1 mm unless otherwise indicated; Baldwin et al. 1931): wing chord length (carpal joint to longest primary feather unflattened; ± 1 mm), tail length (± 1 mm), exposed culmen length (edge of forehead feathers to posterior edge of nail), bill length at nares (posterior edge of nares to posterior edge of nail), total tarsus length (top of bent knee to bottom of foot), bill height (height of upper mandible at nares), and bill width (width of upper mandible at nares). Measurements were taken the same day specimens were collected prior to preparation as museum specimens (fresh measurements), and subsequently 9 months to 2 years after preparation (dry measurements from standard museum round skins) by the same individual (R. E. Wilson) with the same set of calipers. The right wing and tarsus were used for fresh and dry measurements of each specimen. Voucher

[1] Institute of Arctic Biology, Department of Biology and Wildlife, and University of Alaska Museum, University of Alaska, Fairbanks, AK 99775, USA.

[2] Corresponding author; e-mail: ftrew1@uaf.edu

TABLE 1. Effects of shrinkage on body measurements of Cinnamon Teal with correction values from dried specimens to live birds.

Gender	n	Mean length (mm) Fresh	SE	Dry	SE	t[a]	P	Shrinkage %	SE	Correction factor
Males										
Wing chord	80	194.51	1.57	191.00	1.49	8.44	<0.001	2.12	0.25	1.018
Total tarsus	80	41.92	0.26	40.46	0.23	11.21	<0.001	3.43	0.30	1.036
Tail	80	83.04	0.74	93.66	0.95	−0.91	0.366	−0.83	0.83	0.887
Bill nare	80	35.07	0.20	35.08	0.19	−0.04	0.968	−0.03	0.18	1.000
Bill culmen	80	45.63	0.23	45.10	0.26	4.29	<0.001	1.16	0.27	1.012
Bill height	80	13.72	0.09	12.97	0.10	8.01	<0.001	5.36	0.66	1.058
Bill width	80	16.89	0.08	15.95	0.11	11.98	<0.001	6.44	0.54	1.059
Females										
Wing chord	26	189.69	2.88	185.46	2.59	5.25	<0.001	2.17	0.39	1.023
Total tarsus	26	41.56	0.42	39.89	0.42	4.64	<0.001	3.94	0.84	1.042
Tail	26	81.54	1.58	84.49	1.89	−2.35	0.027	−3.73	1.53	0.965
Bill nare	26	32.79	0.28	32.7	0.30	0.71	0.483	0.28	0.38	1.003
Bill culmen	26	43.04	0.38	42.55	0.38	2.54	0.018	1.11	0.44	1.012
Bill height	26	13.06	0.17	12.6	0.20	2.48	0.020	3.45	1.42	1.037
Bill width	26	16.34	0.19	15.3	0.20	5.29	<0.001	6.21	1.15	1.068

[a] *t*-value from paired sample *t*-test.

specimens are archived at the University of Alaska Museum (Fairbanks). A paired *t*-test was used to compare differences between fresh and dry measurements. Pearson correlation values were used to examine the relationship between body mass and percent shrinkage.

RESULTS

Five of the seven measurements for males had significant differences after drying (Table 1). There was no significant change in tail length or bill length at nares, but both measurements showed an increase after drying. All other measurements had >1% decrease with bill height and bill width having the largest shrinkage. Percent shrinkage of total tarsus length (Pearson correlation = 0.255, P = 0.023) and culmen length (Pearson correlation = −0.356, P = 0.001) had a significant relationship with body mass.

Six of the seven body measurements for females had significant differences after drying (Table 1). Bill length at nares had no significant difference. All measurements except tail length decreased after drying with bill width and total tarsus having the greatest amount of shrinkage. There were no significant relationships between any of the shrinkage measurements and body mass.

DISCUSSION

Cinnamon Teal had significant changes after specimen preparation for most measurements. Specimen preparation may have contributed to differences between measurements besides the drying process. The bills of specimens were tied to keep them closed during the drying process in the field. Tying of bills may have squeezed the bill together, slightly decreasing bill width. Tail length increased after drying for House Sparrows (*Passer domesticus*) and was attributed to the retraction of the intercalamal skin (Bjordal 1983).

Bill length is an important descriptor for studying feeding ecology (Borras et al. 2000) and subspecies classification (e.g., Ridgway 1902, Hall 1996). Therefore, it is critical to have a bill measurement that is repeatable and accurate. There are several ways to measure bill length with the three main alternatives being total culmen length, exposed culmen length, and length from the nares (Baldwin et al. 1931). Fjeldså (1980) suggested the amount of shrinkage of the exposed culmen will vary according to bill anatomy and, thus, one universal correction factor would not be applicable to all bird species. This has led to the suggestion that bill length from the posterior edge of the nares is the most reliable

bill measurement as both end points are easily defined (Winker 1998, Borras et al. 2000). This study confirms the recommendation, in particular for waterfowl, that bill length should be measured from the nares, especially if no correction factors are available.

The range of shrinkage values of −3.73 to 6.44% for Cinnamon Teal is comparable to other studies, which report values ranging from −1.5 to 4.0% depending on the body measurement. Correction values to convert dry measurements ranged from 1.000 to 1.068 for measurements that decreased and 0.887 (males, not significant) and 0.965 (females) for tail lengths which increased (Table 1). Winker (1993) suggested correction values that ranged from 0.960 to 0.996 (fresh to dry) which converts to 1.004–1.040 (dry to fresh). No previous data describing specimen shrinkage have been reported for waterfowl to our knowledge; the values reported here provide general correction factors for future studies of morphology in similar sized waterfowl.

ACKNOWLEDGMENTS

We thank Rosario Acero, Raul Clarke, Adrian Contreras, Alejandro Gonzalez, Daniel Ramadori, Karina Ramirez, Sergio Goldfeder, Dirección de Fauna Santa Cruz, Ministerio de la Producción Chubut, Dirección de Fauna Silvestre – Secretaría de Ambiente y Desarrollo Sustentable de la República Argentina, Instituto Nacional de Recursos Naturales del Peru, U.S. Fish and Wildlife Service, California Department of Fish and Game, Edwards Air Force Base, Sonny Bono Salton Sea National Wildlife Refuge (NWR), Oregon Department of Fish and Wildlife, Malheur NWR, Utah Division of Wildlife Resources, Colorado Division of Wildlife, Browns Park NWR, North Dakota Game and Fish Department, and South Dakota Department of Game, Fish, and Parks for authorization to collect waterfowl specimens. We thank Delta Waterfowl Foundation, T. H. Valqui, Larry Janke, and Ambassador Duck Club for aid in specimen collection. Expedition and laboratory costs were funded by the Institute of Arctic Biology at the University of Alaska Fairbanks, National Science Foundation (NSF EPS-0092040, EPS-0346770, and DEB-0444748), grants from the Delta Waterfowl Foundation, Frank M. Chapman Fund at the American Museum of Natural History, and David Burnett Memorial Award to REW. Carla Dove and Sarah Sonsthagen provided helpful comments on this manuscript.

LITERATURE CITED

American Ornithologists' Union (AOU). 1957. Check-list of North American birds. Fifth Edition. American Ornithologists' Union. Baltimore, Maryland, USA.

Baldwin, S. P., H. C. Oberholser, and L. G. Worley. 1931. Measurements of birds. Scientific Publications of the Cleveland Museum of Natural History 2:1–165.

Bjordal, H. 1983. Effects of deep freezing, freeze-drying and skinning on body dimensions of House Sparrows (*Passer domesticus*). Cinclus 6:105–108.

Borras, A., J. Pascual, and J. C. Senar. 2000. What do different bill measures measure and what is the best method to use in granivorous birds? Journal of Field Ornithology 74:606–611.

Delacour, J. 1956. The waterfowl of the world. Volume 2. Country Life Limited, London, United Kingdom.

Fjeldså, J. 1980. Post-mortem changes in measurements of grebes. Bulletin of the British Ornithologists' Club 100:151–154.

Gammonley, J. H. 1996. Cinnamon Teal (*Anas cyanoptera*). The birds of North America. Number 217.

Greenwood, J. G. 1979. Post-mortem shrinkage of Dunlin *Calidris alpina* skins. Bulletin of the British Ornithologists' Club 99:143–145.

Hall, G. A. 1996. Yellow-throated Warbler (*Dendroica domincia*). The birds of North America. Number 223.

Jenni, L. and R. Winkler. 1989. The feather-length of small passerines: a measurement for wing-length in live birds and museum skins. Bird Study 36:1–15.

Johnsgard, P. A. 1978. Ducks, geese, and swans of the world. University of Nebraska Press, Lincoln, USA.

Mueller, H. C. 1990. Can Saw-whet Owls be sexed by external measurements? Journal of Field Ornithology 61:339–346.

Ridgway, R. 1902. The birds of North and Middle America. U.S. National Museum Bulletin 50, Part 2.

Snyder, L. L. and H. G. Lumsden. 1951. Variation in *Anas cyanoptera*. Occasional Papers of the Royal Ontario Museum of Zoology 10:1–18.

Winker, K. 1993. Specimen shrinkage in Tennessee Warblers and "Traill's" Flycatchers. Journal of Field Ornithology 64:331–336.

Winker, K. 1996. Specimen shrinkage versus evolution: I'iwi morphology. Conservation Biology 10: 657–658.

Winker, K. 1998. Suggestions for measuring external characters of birds. Ornithologia Neotropical 9: 23–30.

The Wilson Journal of Ornithology 120(2):393–395, 2008

Breeding Range Extension of the Coastal Plain Swamp Sparrow

Bryan D. Watts,[1,2] Michael D. Wilson,[1] Fletcher M. Smith,[1] Barton J. Paxton,[1] and J. Bill Williams[1]

ABSTRACT.—The Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) is morphologically distinct, restricted to a narrowly-defined habitat type, and geographically isolated within the mid-Atlantic Coastal Plain. The breeding range has been considered to extend from the Nanticoke River in Maryland north to the Hudson River. We report a previously undocumented population near Warsaw, Virginia that extends the known range south and west into a region of the Chesapeake Bay with extensive tidal fresh and brackish marshes consistent with the habitat requirements of this form, but for which there has been no documented breeding. A broader investigation of occurrence within appropriate habitat seems warranted given the small global population size and uncertain status within the southern portion of its range. *Received 9 November 2006. Accepted 2 August 2007.*

The Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) is restricted to tidal fresh and brackish marshes of the mid-Atlantic coast. The form is distinctive in having a larger bill, grayer plumage, and more black in the crown and nape compared to other Swamp Sparrows (Bond and Stewart 1951, Greenberg and Droege 1990). Breeding populations appear to use a limited range of habitats that contain a mix of marsh vegetation and shrubs with a characteristic structure that typically forms along the marsh-upland interface (Meanley 1975, Beadell et al. 2003)

The known breeding distribution of the Coastal Plain Swamp Sparrow has been extended over time as expanded survey efforts have discovered new breeding locations. The subspecies was initially described from several specimens from the Nanticoke River near Vienna, Maryland (Bond and Stewart 1951). Investigations have extended the range west to near Washington, D.C. and north to the mouth of the Hudson River (Stewart and Robbins 1958, Greenberg and Droege 1990, Droege and Blom 1996). The breeding range since 1957 has been described to extend from the Nanticoke River in Maryland north to the Hudson River (AOU 1957, Mowbray 1997). Beadell et al. (2003), in a recent evaluation of the breeding population, established a center of abundance around Delaware Bay and the Tuckahoe and Mullica rivers in coastal New Jersey. Greenberg and Droege (1990), in an earlier review of the breeding range, reported no evidence of breeding south of Maryland. Clapp (1997) reported no confirmed breeding records for coastal Virginia. Here, we report on a previously undocumented population of *M. g. nigrescens* near Warsaw, Virginia.

METHODS

Mulberry Point Marsh (37° 59′ 30″ N, 76° 53′ 35″ E) is 178 ha along the oligohaline reach of the Rappahannock River near Warsaw, Virginia. Vegetation within the marsh is dominated by big cordgrass (*Spartina cynosuroides*), salt meadow hay (*S. patens*), marsh hibiscus (*Hibiscus moscheutos*), cattail (*Typha augustifolia*), and olney threesquare (*Scirpus olneyi*) with a diverse mixture of other marsh species. The marsh contains numerous tree and shrub hummocks. Historically, parts of the marsh have been used for agriculture and cattle grazing, and the marsh is disturbed by a roadway, a dike system, and limited ditching. These alterations along with the natural hummocks create topographic variation, habitat diversity, and an extensive network of marsh-upland ecotones. Normal tidal variation along this reach of the river is ~0.5 m.

We received a report of 14 birds within the marsh during June 2004 (F. T. Atwood, pers. comm.) and conducted a spot-mapping effort between 24 May and 13 June 2005 to: (1) estimate population size, and (2) document breeding. We systematically walked throughout the entire marsh surface twice and mapped

[1] Center for Conservation Biology, College of William and Mary, Williamsburg, VA 23187, USA.

[2] Corresponding author; e-mail: bdwatt@wm.edu

locations of all singing males on aerial photographs. The overall number of singing males and their approximate locations were consistent between surveys. We assumed the number of singing males provided a good estimate of the breeding population but made no attempt to identify their pairing status. We spent ~2 hrs on 24 May observing birds to locate nests for a limited number of pairs. We did not follow nests through time to ascertain breeding success.

OBSERVATIONS

We mapped 41 singing male Coastal Plain Swamp Sparrows that appeared to be defending discrete territories. Birds were not evenly distributed throughout the marsh but were concentrated within patches containing threesquare and scattered groundsel (*Baccharis halimifolia*) trees. All patches of any size (>0.25 ha) of this habitat supported birds. Patches comprised entirely of taller vegetation (e.g., big cordgrass) were not occupied. Singing males perched on shrubs within the meadow vegetation or on trees or shrubs along the edge of meadows. We located five active nests during the morning of 24 May. These included two nests under construction and one nest each with 2, 3, and 4 eggs, respectively. All nests were at or near the base of groundsel trees and hidden in clusters of newly emerging leaves.

DISCUSSION

Documentation of the Mulberry Point Marsh population of Coastal Plain Swamp Sparrows extends the known breeding range south into Virginia. The site is 90 km west and 30 km south of the Nanticoke River in Maryland. More importantly, this site is within the lower western shore of Chesapeake Bay, a region with extensive tidal fresh and brackish marshes consistent with the habitat requirements of this form, but for which there has been no documented breeding. The size of the population places it among the largest currently known in the Chesapeake Bay portion of the range. A cursory survey of Island Farm Marsh, 8 km down river from Mulberry Point on 14 July 2005 resulted in the location of 5 singing males. Documentation of birds at a second site suggests the possibility that breeding may be more extensive than currently known.

The Coastal Plain Swamp Sparrow appears to be morphologically distinct, geographically isolated, and specialized in a narrowly-defined habitat type. These are characteristics of other sparrow forms such as the Dusky Seaside Sparrow (*Ammodramus maritimus nigrescens*) (Sykes 1980), Cape Sable Seaside Sparrow (*A. maritimus mirabilis*) (Pimm et al. 1996), and Ipswich Savannah Sparrow (*Passerculus sandwichensis princeps*) (Smith et al. 2003) that were extirpated or have been of high conservation concern in recent decades. A recent assessment of the population of Coastal Plain Swamp Sparrow within Maryland, Delaware, and New Jersey resulted in a conservative estimate of 28,000 pairs and suggested a decline in both abundance and distribution along the western shore and lower eastern shore of the Chesapeake Bay (Beadell et al. 2003). Given the uncertain status of this form in the southern portion of its range, a broad investigation of occurrence within appropriate habitat seems warranted. Consideration of listing of the Coastal Plain Swamp Sparrow by appropriate agencies and jurisdictions as a species of conservation concern may facilitate conservation efforts.

ACKNOWLEDGMENTS

We thank F. T. Atwood for early reports of this population, A. M. France for allowing access to the site, M. U. Watts for assisting with surveys on Mulberry Point Marsh, and S. C. Spencer for assistance with surveys of Island Farm Marsh. R. B. Clapp and Sam Droege made helpful comments on an earlier draft of this manuscript. This study was funded by the Center for Conservation Biology at the College of William and Mary.

LITERATURE CITED

American Ornithologists' Union (AOU). 1957. Check-list of North American birds. Fifth Edition. American Ornithologists' Union, Washington, D.C., USA.

Beadell, J., R. Greenberg, S. Droege, and J. A. Royle. 2003. Distribution, abundance, and habitat affinities of the Coastal Plain Swamp Sparrow. Wilson Bulletin 115:38–44.

Bond, G. M. and R. E. Stewart. 1951. A new Swamp Sparrow from the Maryland Coastal Plain. Wilson Bulletin 63:38–40.

Clapp, R. B. 1997. Egg dates for Virginia birds. Virginia Avifauna 6. Virginia Society of Ornithology, Lynchburg, USA.

Droege, S. and E. A. T. Blom. 1996. Swamp Sparrow (*Melospiza georgiana*). Pages 408–409 *in* Atlas of the breeding birds of Maryland and the District of Columbia (C. S. Robbins, Senior Editor). University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.

Greenberg, R. and S. Droege. 1990. Adaptations to tidal marshes in breeding populations of the Swamp Sparrow. Condor 92:393–404.

Meanley, B. 1975. Birds and marshes of the Chesapeake Bay country. Tidewater Publishers, Cambridge, Maryland, USA.

Mowbray, T. B. 1997. Swamp Sparrow (*Melospiza georgiana*). The birds of North America. Number 279.

Pimm, S., J. Curnutt, J. Lockwood, L. Manne, A. Mayner, M. Nott, and K. Balent. 1996. Population ecology of the Cape Sable Sparrow (*Ammodramus maritimus mirabilis*): annual report, 1996. USDI, National Biological Survey/National Park Service, Everglades National Park, Homestead, Florida, USA.

Smith, J. S., Z. Lucas, and W. T. Stobo. 2003. Estimate of the Ipswich Sparrow population on Sable Island, Nova Scotia, in 1998, using random-transect survey design. Canadian Journal of Zoology 81:771–779.

Stewart, R. E. and C. S. Robbins. 1958. Birds of Maryland and the District of Columbia. North American Fauna 62. USDI, Fish and Wildlife Service, Washington, D.C., USA.

Sykes, P. W. 1980. Decline and disappearance of the Dusky Seaside Sparrow from Merritt Island, Florida. American Birds 34:728–737.

The Wilson Journal of Ornithology 120(2):395–398, 2008

Polyandry and Sex Ratio in the Song Sparrow

Michael H. Janssen,[1] Peter Arcese,[1,2] Mark S. Sloan,[1] and Kelly J. Jewell[1]

ABSTRACT.—Polyandry occurs when females form social bonds and gain simultaneous parental care from multiple male mates. It is thought to be rare in birds and to occur more often in territorial species when the Operational Sex Ratio (OSR; ratio of mature males to females) exceeds one. We asked if variation in the OSR affected the rate of polyandry in Song Sparrows (*Melospiza melodia*) over 30 years on Mandarte Island, British Columbia, Canada. We found no correlation between OSR and polyandry (R_s = 0.04, df = 28, P = 0.86), but positive correlations between OSR and percent females with more than one social mate (R_s = 0.44, df = 28, P = 0.01), and percent females sharing a territory with a replacement male and her dependent young (R_s = 0.46, df = 28, P = 0.009). We suggest that polyandry in Song Sparrows is limited by the intolerance of territorial males towards intruders, but that it occurs when females occupy the territories of two or more males and gain their simultaneous care for the dependent young of a single brood as a consequence. *Received 2 October 2006. Accepted 25 July 2007.*

Cooperative polyandry, wherein two or more males mate with one female and contribute care to a single brood, is rare in birds (Jenni 1974, Oring 1986). However, in species that compete to defend breeding territories, the frequency of polygamy is often related to the 'Operational Sex Ratio' (OSR, ratio of mature males to females in a population; Emlen and Oring 1977, Davies and Lundberg 1984, Lank et al. 1985, Reynolds 1987, Wiktander et al. 2000, Pilastro et al. 2001). Thus, it is possible that polyandry is rare in some species either because the OSR is rarely skewed sufficiently to favor it or because territory defense by males prevents females from receiving the care of two males at one nest simultaneously (Arcese 1989a).

Song Sparrows (*Melospiza melodia*), often considered to be monogamous (e.g., Verner and Willson 1966), are now known to engage regularly in genetic polyandry (O'Connor et al. 2006) and social polygyny, the latter being more common when OSR favors females (Smith et al. 1982, Arcese 1989a). We describe the first cases of cooperative polyandry in Song Sparrows and ask if variation in the OSR predicted their occurrence over 30 years on Mandarte Island, British Columbia, Canada. We expected that OSRs favoring males would increase the rate of polyandry, unless territoriality prevented multiple males from feeding one brood simultaneously.

[1] Centre for Applied Conservation Research, University of British Columbia, Forest Sciences Centre, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

[2] Corresponding author; e-mail: peter.arcese@ubc.ca

METHODS

Study Area.—Mandarte is a ~6-ha islet about 10 km southeast of Sidney, British Columbia where Song Sparrows have been studied continuously since 1975 (Smith et al. 2006). Song Sparrows on Mandarte Island nest mainly in shrub patches that cover about a third of the islet, are individually marked, and defend territories year-round with peaks in aggression in fall and late winter through spring. Territories were mapped annually and the breeding status of all adults was assessed each 3–7 days from March or April to the end of breeding from 1975 to 2005 (except 1980; see Smith et al. 2006).

Mated and Territorial Status of Males.—We recorded instances from 1975 to 2005 where more than one male was observed feeding young from one brood simultaneously or sequentially in the course of a female's nesting cycle. We choose feeding by males as the main criteria for polyandry because 'pair bonds' are difficult to quantify and genetic evidence was available in only 4 years. Although extra-pair fertilization and mate switching are common in Song Sparrows (Arcese et al. 2002, O'Connor et al. 2006), neither constitute polyandry (Oring 1986). In contrast, cases in which females gain parental care from and maintain social contact with two males simultaneously are generally considered to be polyandrous (Jenni 1974, Oring 1986), and were defined by us as engaging in 'cooperative polyandry'. In contrast, we defined cases wherein males fed young from single broods sequentially, such as after a territory take-over (Arcese 1989b), as 'sequential polyandry'. We also recorded instances wherein a male neighbor or replacement without young of their own carried food to young on a neighboring or newly acquired territory or were followed persistently by begging young, as suspected cases of sequential or cooperative polyandry. OSR equaled the ratio of sexually mature adult males to females alive in late April each year.

Statistical Analyses.—We used SYSTAT 11.0 for all analyses (Systat Software Inc., Point Richmond, CA, USA) and Spearman's rank correlation to test for links between OSR and the frequency of polyandry, the percent of females with more than one social mate in a year, the percent of females whose young came into contact with a replacement male, and rate of 'adoption' (feeding) by replacement males. Frequency data were analyzed by Chi-square with the Yates correction applied.

RESULTS

On average (± SD), 16 ± 9% of females (range = 0–37%) occupied territories with two or more social mates annually from 1975 to 2005. Females gained new social mates by occupying two or more territories within a breeding season (55 cases) or forming social bonds with replacement males after a territory take-over (111 cases); the latter occurring more often ($\chi^2_{yates} = 15.8$, df = 1, $P < 0.001$). Eighteen of 72 males (25%) were known or suspected to have fed fledglings that remained on their natal territory after the replacement male's arrival.

Cooperative polyandry was confirmed once and suspected twice, but sequential polyandry was more common with seven confirmed and eight suspected cases. Overall, 3.7% of 492 females and 6.5% of 505 males that bred during 1975 to 2005, bred at least once in a polyandrous group. Three males were recorded in polyandrous associations twice in their lifetimes.

One case of cooperative polyandry was observed in detail in May 2005. On 24 April, two young hatched in a nest on the territory of male M1 and female F1. On 4 May, M1 lost part of this territory to neighbor M2. Rather than remaining in M1's territory, however, F1 occupied both territories and interacted with both M1 and M2, which each fed one of F1's fledglings to independence on about 23 May. F1 laid the first egg of her second nest inside M2's territory on 12 May. Two suspected cases of cooperative polyandry also occurred when females expanded their range to occupy the territories of unpaired males with two fledglings tended by her new social mate and one by the previous social mate.

Sequential polyandry occurred in two ways. In three cases, females moved to a neighbor's territory with all her dependent fledglings. In 12 cases, replacement males occupied the territories of females with dependent young. In all 15 cases, both males fed young from a single female's brood sequentially.

Contrary to expectation, OSR and annual

percent of females in suspected or confirmed cases of polyandry were unrelated (R_s = 0.04, df = 28, P = 0.86). OSR was related positively to the percent of females that had more than one social mate in a year (R_s = 0.44, df = 28, P = 0.01), and to the percent of females that mated with replacement males while still caring for the fledglings of a prior mate (R_s = 0.46, df = 28, P = 0.009). The proportion of replacement males that fed dependent young alive at the time they occupied their new territory was also unrelated to the OSR (R_s = 0.04, df = 28, P = 0.83).

Fifteen of 18 (83%) males known or suspected to have fed their new mate's young were previously the female's neighbor, but three polyandrous males were non-territorial floaters. Thus, many polyandrous males probably interacted socially with females whose young they later fed prior to the time they began sharing a territory. However, in 43 cases where polyandry could have been detected, neighbors were not more likely to feed the young of a previous male than were floaters (43% of 35 vs. 38% of 8 cases, respectively).

DISCUSSION

Polyandry was rare among Song Sparrows on Mandarte Island but did occur when females with dependent fledglings occupied the territories of adjacent males and received simultaneous parental care from those males as a result. Over 30 years, 3.7% of females and 6.5% of males bred in cooperative or sequentially polyandrous groups at least once, compared to 21% of females and 13% of males exposed to polygyny (Arcese 1989a).

We found no relation between the OSR and frequency of polyandry, perhaps because it occurred so rarely. However, percent females paired to more than one male in a season, and percent fledglings occupying a territory with a replacement male, each increased with the OSR. These results suggest the availability of unmated males and level of male competition affect female breeding dispersal and male replacement, but they are contrary to the idea that OSR affects polyandry.

Emlen and Oring (1977) predicted that polyandry will occur more often when adult sex ratios favor males; an idea well-supported in *Prunella*, where polyandry is relatively common at OSR's as extreme as 1.48 (*P. modularis*; Davies and Lundberg 1984) and 1.38 (*P. collaris*; Davies et al. 1995). In contrast, polyandry was rare in Song Sparrows on Mandarte Island even though the OSR averaged 1.67 ± 0.66 (SD, n = 30 years) and exceeded 2.50 in 3 years. We suggest this difference between species arises as a consequence of intolerance by territorial male Song Sparrows toward intruders.

Whereas males of many polyandrous species feed young from a single brood within the bounds of one territory (Davies and Lundberg 1984, Hartley and Davies 1994, Briskie et al. 1998, Goetz et al. 2003), intolerance by male Song Sparrows may prevent genetically polyandrous males from simultaneously feeding their young except when they are divided among adjacent territories. O'Connor et al. (2006) noted that ~27% of nestling Song Sparrows on Mandarte Island were fathered by males other than the social mate and that most extra-pair males were neighbors. Most (86%) polyandrous males we identified were also neighbors of the female whose young they later fed. Thus, it is possible that male Song Sparrows fed young from adjacent territories according to their confidence of paternity (e.g., Davies and Hatchwell 1992). If true, extra-pair males might also be expected to engage more often in vigilance and alarm calling while their extra-pair mates incubate or tend nestlings in an adjacent territory.

ACKNOWLEDGMENTS

Our work was funded by the National Science and Engineering Research Council of Canada, U.S. National Science Foundation, and the generous support of Werner and Hildegard Hesse. Many people contributed to data collection, including most recently Laura Sampson, and Scott and Amy Wilson. Patricia Janssen and two anonymous reviewers provided helpful comments, and the Tswaout and Tseycum bands kindly facilitated our work on Mandarte Island.

LITERATURE CITED

Arcese, P. 1989a. Intrasexual competition and the mating system in primarily monogamous birds: the case of the Song Sparrow. Animal Behaviour 38: 96–111.

Arcese, P. 1989b. Territory acquisition and loss in the Song Sparrow. Animal Behaviour 37:45–55.

Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten. 2002. Song Sparrow (*Melospiza melodia*). The birds of North America. Number 704.

Briskie, J. V., R. Montgomerie, T. Poldmaa, and P.

T. Boag. 1998. Paternity and paternal care in the polygynandrous Smith's Longspur. Behavioral Ecology and Sociobiology 43:181–190.

Davies, N. B. and B. J. Hatchwell. 1992. The value of male parental care and its influence on reproductive allocation by male and female Dunnocks. Journal of Animal Ecology 61:259–272.

Davies, N. B. and A. Lundberg. 1984. Food distribution and a variable mating system in the Dunnock, *Prunella modularis*. Journal of Animal Ecology 53:895–912.

Davies, N. B, I. R. Hartley, B. J. Hatchwell, A. Desrochers, J. Skeer, and D. Nebel. 1995. The polygynandrous mating system of the Alpine Accentor, *Prunella collaris*. I. Ecological causes and reproductive conflicts. Animal Behaviour 49:769–788.

Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215–223.

Goetz, J. E., K. P. McFarland, and C. C. Rimmer. 2003. Multiple paternity and multiple male feeders in Bicknell's Thrush (*Catharus bicknelli*). Auk 120:1044–1053.

Hartley, I. R. and N. B. Davies. 1994. Limits to polyandry in birds. Proceedings of the Royal Society of London, Series B 257:67–73.

Jenni, D. A. 1974. Evolution of polyandry in birds. American Zoologist 14:129–144.

Lank, D. B., L. W. Oring, and S. J. Maxson. 1985. Mate and nutrient limitation of egg-laying in a polyandrous shorebird. Ecology 66:1513–1524.

O'Connor, K. D., A. B. Marr, P. Arcese, L. F. Keller, K. J. Jeffery, and M. W. Bruford. 2006. Extra-pair fertilization and effective population size in the Song Sparrow (*Melospiza melodia*). Journal of Avian Biology 37:572–578.

Oring, L. W. 1986. Avian polyandry. Current Ornithology 3:309–351.

Pilastro, A., L. Biddau, G. Marin, and T. Mingozzi. 2001. Female brood desertion increases with number of available mates in the Rock Sparrow. Journal of Avian Biology 32:68–72.

Reynolds, J. D. 1987. Mating system and nesting biology of the Red-necked Phalarope *Phalaropus lobatus*: what constrains polyandry? Ibis 129:225–242.

Smith, J. N. M, Y. Yom-Tov, and R. Moses. 1982. Polygyny, male parental care, and sex ratio in Song Sparrows: an experimental study. Auk 99: 555–564.

Smith, J. N. M., L. F. Keller, A. B. Marr, and P. Arcese. 2006. Biology of small populations: the Song Sparrows of Mandarte Island. Oxford University Press, New York, USA.

Verner, J. and M. F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology 47:143–147.

Wiktander, U., O. Olsson, and S. G. Nilsson. 2000. Parental care and social system in the Lesser Spotted Woodpecker *Dendrocopus minor*. Journal of Avian Biology 31:447–456.

The Wilson Journal of Ornithology 120(2):398–401, 2008

Novel Courtship Behavior in the Little Greenbul (*Andropadus virens*)

Alexander N. G. Kirschel[1]

ABSTRACT.—The Little Greenbul (*Andropadus virens*) is a common African forest bird that is thought to form monogamous pair bonds. In March 2007, I observed a male hanging below a presumed female perched on a branch, apparently inspecting her cloaca and clinging to her when she flew from that branch, while singing throughout. This apparent mate guarding behavior suggests that extra-pair fertilizations may occur in this species. *Received 3 May 2007. Accepted 11 September 2007.*

Extra-pair paternity (EPP) is a widespread phenomenon in socially monogamous birds (Birkhead et al. 1987) and has been documented for many temperate bird species, such as Great Reed Warbler (*Acrocephalus arundinaceus*) (Hasselquist et al. 1996). It has also been reported for tropical species, such as Blue-black Grassquit (*Volatinia jacarina*) (Carvalho et al. 2006) and Red-backed Fairywren (*Malurus melanocephalus*) (Karubian 2002). There appears to be no general rule that explains the occurrence of EPPs across socially monogamous species (Griffith et al. 2002, Westneat and Stewart 2003).

Males also sire young of multiple females in species with polygynandrous mating systems such as Dunnock (*Prunella modularis*) (Davies 1983), the related Alpine Accentor (*P. collaris*), and the unrelated Smith's Longspur (*Calcarius pictus*) (Birkhead et al. 1993). Po-

[1] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA; e-mail: kirschel@ucla.edu

lygynandrous species also have much larger cloacal protuberances than socially monogamous species (Briskie 1993).

Davies (1983) described the unusual behavior of cloaca-pecking in the polygynandrous Dunnock in which males peck female cloacas to induce release of sperm from other males. To my knowledge this is the only example of male birds stimulating the ejection of sperm when its paternity is in doubt. Females, however, eject sperm from subordinate males in feral fowl (*Gallus gallus*) (Pizzari and Birkhead 2000), and when sperm is old and degraded in Black-legged Kittiwakes (*Rissa tridactyla*) (Wagner et al. 2004). Males of several bird species are known to eject eggs from nests when EPPs are suspected (e.g., Sand Martins [*Riparia riparia*] [Alves and Bryant 1998] and Blue-footed Boobies [*Sula nebouxii*] [Osorio-Beristain and Drummond 2001]).

The Little Greenbul (*Andropadus virens*, Pycnonotidae) is a common African forest passerine that occurs in primary and secondary tropical rainforest, forest edges, and gallery forest in sub-Saharan Africa. Previous work has documented variation in Little Greenbul morphology and song across an ecological gradient (Smith et al. 1997, Slabbekoorn and Smith 2002), but less is known about its breeding behavior. It has traditionally been described as a territorial breeder (Fishpool and Tobias 2005) with males competing for territories by singing all day during the breeding season. Playback experiments indicate that males respond strongly to the potential threat of conspecific intruders by approaching close to or flying noisily above or past a loudspeaker projecting conspecific song. Males may also change their song performance in response to playback by singing back more continuously or falling completely silent (A. N. G. Kirschel, unpubl. data). The objective of this paper is to describe courtship behavior in the Little Greenbul that could imply the occurrence of EPPs or an alternative mating strategy such as polygynandry.

OBSERVATIONS

I observed an apparently novel behavior between two Little Greenbuls on the morning of 23 March 2007 while recording the song of a male at the Limbe Botanic Gardens in Cameroon (4° 0′ N, 9° 12′ E). A singing male was hanging upside-down from a horizontal branch behind a perched bird, presumed to be a female. The male was flapping his wings continuously to remain suspended from the branch. His head was facing the rear end of the perched bird and he appeared to be inspecting its cloaca (Fig. 1). The male remained in this suspended position, singing intermittently, for several minutes while the perched bird remained on the branch apparently unperturbed. Both birds flew to one branch and then another after 5 min of recording with the singing male clutching on to the back of the suspected female in flight. Shortly thereafter the two birds separated.

DISCUSSION

This was a single observation of a behavior not previously reported. I posit the territorial male was inspecting the female as part of a mate guarding strategy, perhaps investigating for evidence of extra-pair copulations. It became more difficult to observe the two birds when they started moving to other perches and I did not observe copulation. This observation suggests the mating system of the Little Greenbul may be more complex than previously understood. Male Little Greenbuls spend so much time singing that females could have opportunities to move to neighboring territories to seek extra-pair fertilizations from males they perceive to be superior. This behavior has been reported for Great Reed Warblers where females moved through several territories before choosing a male; male reproductive success was correlated with song repertoire size (Hasselquist et al. 1996). The cloaca inspection behavior could represent high levels of EPP and social monogamy in the Little Greenbul or it could represent an alternative mating strategy, such as polygynandry.

The Little Greenbul's presumed sister taxon, the Yellow-whiskered Greenbul (*Andropadus latirostris*), is known to have a complex mating system. Males display in leks where they occur at high densities, at least in parts of the species' range, but are territorially monogamous at lower densities (Fishpool and Tobias 2005). The only record of courtship behavior in the Little Greenbul involved a singing male beating its wings, slightly lowering its tail, and puffing its throat as a suspected female approached through the foliage (Keith

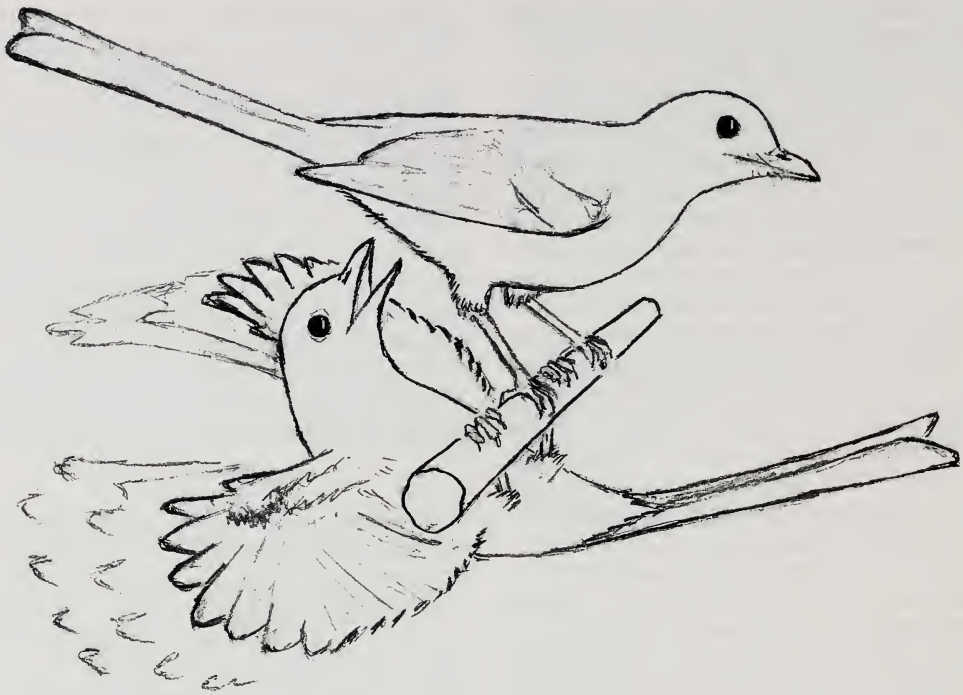


FIG. 1. Male Little Greenbul suspended from a branch inspecting the rear of a presumed female, while singing. The observed birds were in approximately this position at the Limbe Botanic Gardens in Cameroon with the male clinging either to the branch or perhaps the toes of the upper bird, while moving its head up and out of view behind the perched bird.

1992). Gatherings of 6–10 singing males are not thought to represent lekking behavior because there is no evidence of site fidelity in these congregations (Brosset and Erard 1986, Fishpool and Tobias 2005). Brosset and Erard (1986) also described the Little Greenbul as nomadic and rarely territorial, suggesting song might have a greater role in sexual selection than territory defense. Further behavioral studies, and perhaps a comparison of cloacal protuberances with other species, are needed to gain a better understanding of the Little Greenbul's mating system. Moreover, work is needed to ascertain whether the courtship behavior observed in Cameroon is a novel behavior in birds or convergent to the cloaca-pecking strategy of mate guarding.

ACKNOWLEDGMENTS

I thank Neil Losin for his illustration of the Little Greenbul behavior I observed, and Ndje Francis for assistance in the field at Limbe Botanic Gardens. I thank D. T. Blumstein and T. B. Smith for assistance with funding, and Hans Slabbekoorn, Jordan Karubian, Brittany Enzmann, Neil Losin, Lincoln Fishpool, and one anonymous reviewer for helpful comments on the manuscript.

LITERATURE CITED

ALVES, M. A. S. AND D. M. BRYANT. 1998. Brood parasitism in the Sand Martin, *Riparia riparia*: evidence for two parasitic strategies in a colonial passerine. Animal Behaviour 56:1323–1331.

BIRKHEAD, T. R., L. ATKIN, AND A. P. MØLLER. 1987. Copulation behavior of birds. Behavior 101:101–138.

BIRKHEAD, T. R., J. V. BRISKIE, AND A. P. MØLLER. 1993. Male sperm reserves and copulation frequency in birds. Behavioral Ecology and Sociobiology 32:85–93.

BRISKIE, J. V. 1993. Anatomical adaptations to sperm competition in Smith's Longspurs and other polygynandrous passerines. Auk 110:875–888.

BROSSET, A. AND C. ERARD. 1986. Les Oiseaux des région forestières du nord-est de Gabon. Volume 1. Ecologie et comportement des espèces. Société Nationale de Protection de la Nature, Paris, France.

CARVALHO, C. B. V., R. H. MACEDO, AND J. A. GRAVES. 2006. Breeding strategies of a socially monogamous neotropical passerine: extra-pair fertilizations, behavior, and morphology. Condor 108:579–590.

Davies, N. B. 1983. Polyandry, cloaca-pecking and sperm competition in Dunnocks. Nature 302:334.

Fishpool, L. D. C. and J. A. Tobias. 2005. Family Pycnonotidae (bulbuls). Pages 124–250 *in* Handbook of the birds of the world. Volume 10 (Cuckoo-shrikes to thrushes) (J. del Hoyo, A. Elliot, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Griffith, S. C., I. P. F. Owens, and K. A. Thuman. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Molecular Ecology 11:2195–2212.

Hasselquist, D., S. Bensch, and T. von Schantz. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the Great Reed Warbler. Nature 381:229–232.

Karubian, J. 2002. Costs and benefits of variable breeding plumage in the Red-backed Fairy-wren. Evolution 56:1673–1682.

Keith, S. 1992. Pycnonotidae, bulbuls. Pages 279–377 *in* The birds of Africa. Volume 4. (S. Keith, E. K. Urban, and C. H. Fry, Editors). Academic Press, London, United Kingdom.

Osorio-Beristain, H. and H. Drummond. 2001. Male boobies expel eggs when paternity is in doubt. Behavioral Ecology 12:16–21.

Pizzari, T. and T. R. Birkhead. 2000. Female feral fowl eject sperm of subdominant males. Nature 405:787–789.

Slabbekoorn, H. and T. B. Smith. 2002. Habitat-dependent song divergence in the Little Greenbul: an analysis of environmental selection pressures on acoustic signals. Evolution 56:1849–1858.

Smith, T. B., R. K. Wayne, D. J. Girman, and M. W. Bruford. 1997. A role for ecotones in generating rainforest biodiversity. Science 276:1855–1857.

Wagner, R. H., F. Helfenstein, and E. Danchin. 2004. Female choice of young sperm in a genetically monogamous bird. Proceedings of the Royal Society of London Series B-Biological Sciences 271:S134–S137.

Westneat, D. F. and I. R. K. Stewart. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annual Review of Ecology, Evolution, and Systematics 34:365–396.

The Wilson Journal of Ornithology 120(2):401–403, 2008

A Recording of a Type B Song of the Yellow-throated Warbler

Bailey D. McKay[1]

ABSTRACT.—On 28 April 2006 in Ohio and again on 19 May 2006 in North Carolina, I observed and, on the April occasion, recorded a Yellow-throated Warbler (*Dendroica dominica*) singing a type B song. A sound spectrogram of this rare song is compared with the more common type A song of this species. I present evidence that my recording is a type B song and speculate on the rare condition and function of this song. *Received 15 February 2007. Accepted 19 July 2007.*

The Yellow-throated Warbler (*Dendroica dominica*) is a common neotropical migrant that breeds in the southeastern United States (Hall 1996). Its song is described by Peterson (2002: 230) as "a series of clear slurred notes dropping slightly in pitch." Most males sing only one song, but there are a few reports of Yellow-throated Warblers singing a second song (Hall 1996). The second song has been described as more musical than the type A song and consisting of four notes on the same pitch, three descending, and ending with one on a higher pitch (Nice 1931). It is not known whether this second song functions like a type B song (*sensu* Spector 1992). The objective of this paper is to: (1) describe the type B song of the Yellow-throated Warbler and (2) report on the context in which this song was observed.

OBSERVATIONS

On 28 April 2006 in Lawrence County, Ohio and again on 19 May 2006 in Graham County, North Carolina I observed Yellow-throated Warblers, one at each site, singing an atypical song. In accordance with the infrequent reports of a second Yellow-throated Warbler song, I only heard two individuals singing this song during an estimated 400 hrs of fieldwork with this species during two seasons. Both observations occurred at dusk around 1930 hrs and, in both cases, the sing-

[1] Department of Biological Sciences, Auburn University, Auburn, AL 36849, USA; e-mail: mckaybd@auburn.edu

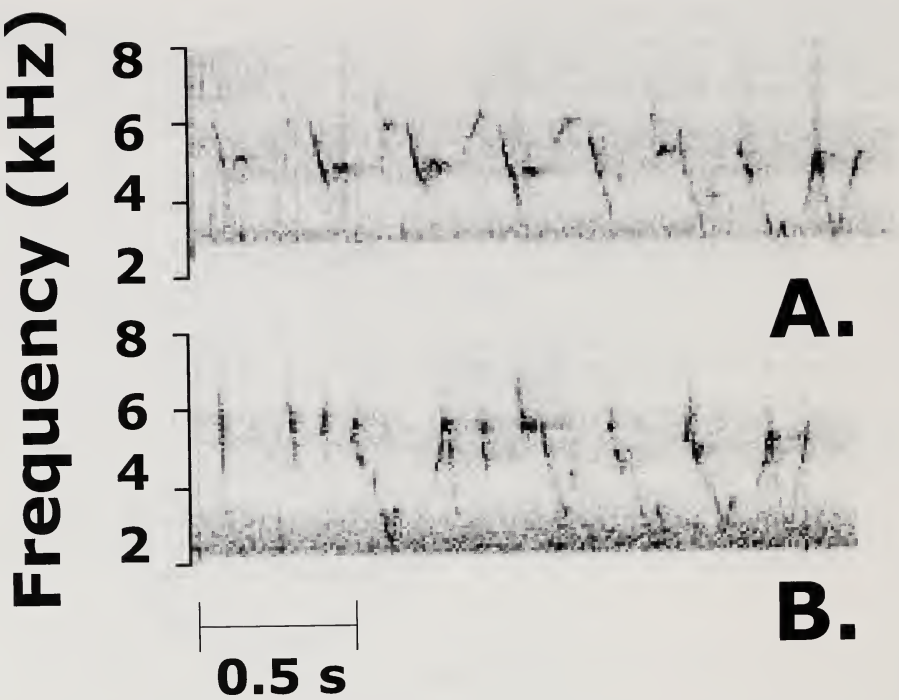


FIG. 1. Spectrograms of the two Yellow-throated Warbler song types as sung by a breeding male in Lawrence County, Ohio. A. Type A song. B. Type B song. Sound below 2 kHz was removed from the spectrogram to eliminate visually distracting background noise.

ing birds mixed chip-like call notes with the song. I recorded the Ohio bird singing this song, which, to the best of my knowledge, is the first recording of the type B song of the Yellow-throated Warbler.

I made a sound spectrogram of the type B song (Fig. 1B) using program Syrinx and compared it to the more common type A song as sung by the same bird (Fig. 1A). Comparison of the two song types reveals the repeated descending note that dominates the type A song is incorporated into the second song. For example, the last phrase, consisting of several descending notes followed by an ascending note, is similar in both songs. The introduction, however, differs between songs. The type B song is less accented with a single descending introductory note followed by two slightly down-slurred notes and a note that is again similar to the descending note in the type A song. This phrase is repeated and followed by the last phrase which is similar to the last phrase of the type A song. Raw recordings of all the songs discussed are available from the author.

DISCUSSION

The type B song (Fig. 1B) is consistent with the only description of a Yellow-throated Warbler second song (Nice 1931) in that it contains several notes on the same pitch (although these are mixed with slurred notes) and four descending notes followed by one that is an upsweep, or a rising note. In addition to matching the only description of the Yellow-throated Warbler second song, evidence the observations I am reporting are type B songs include details common to both observations which fit the pattern of type B song use outlined by Spector (1992). For example, both instances occurred at dusk when the type B song is more frequent and the type A song is usually absent (Spector 1992). The birds in both cases sang type B songs in rapid succession and mixed chip-like call notes between songs, which are characteristics associated with type B songs for *Dendroica* species (Spector 1992). Type B songs typically increase in frequency later in the breeding season (Spector 1992) and both of my observa-

tions came rather late in the breeding season for Yellow-throated Warblers, which begin nesting earlier than most neotropical migrants (Hall 1996).

The context of my observations also agrees with a general pattern of type B song function (Spector 1992). The Yellow-throated Warbler is relatively habitat-specific and, in the eastern portion of its range, prefers the canopy of mature pine (*Pinus* spp.) stands consisting of ~a dozen trees (pers. obs.). This habitat configuration seems to be most common in isolated patches within young deciduous forests. In the west, this bird prefers sycamore (*Platanus* spp.) trees along stream bottoms or mature bald cypress trees (*Taxodium* spp.) within a swamp (Hall 1996). All of these circumstances cause Yellow-throated Warbler occurrence to be patchy and it is rare to find more than 2–3 singing individuals within earshot of one another (pers. obs.). The type B song functions in male-male interactions in most *Dendroica* species and I propose the patchy distribution of breeding males within appropriate habitat make Yellow-throated Warbler male-male interactions less frequent. This has made the need for a type B song uncommon in this species. This idea appears to be corroborated by the context in which I observed this rare type B song. In both cases, the song was observed where Yellow-throated Warbler density was unusually high. In Ohio, I could hear six singing Yellow-throated Warbler males from the spot I recorded the type B song. Likewise, in North Carolina, Yellow-throated Warbler density was the highest I have observed, and I could hear seven singing males from where I heard the type B song. I conducted field work with Yellow-throated Warblers at eight other sites in seven states and did not hear this song at any of these locations, where I could not hear more than four, and usually no more than two, males singing from any one location.

The bird in Ohio belonged to the western *D. d. albilora* subspecies whereas the bird in North Carolina belonged to the eastern *D. d. dominica* subspecies indicating that a second singing behavior in the Yellow-throated Warbler continues to function in both of its major subspecies. I predict the type B song is more common in the western *albilora* group as the densities of this warbler are generally higher there than in the east.

ACKNOWLEDGMENTS

This research was funded through a Frank M. Chapman grant from the American Museum of Natural History. The Hill Laboratory made helpful comments on the manuscript as did reviewers Jill Soba and D. A. Spector.

LITERATURE CITED

Hall, G. A. 1996. Yellow-throated Warbler (*Dendroica dominica*). The birds of North America. Number 223.

Nice, M. M. 1931. The birds of Oklahoma. Revised Edition. University of Oklahoma Press, Norman, USA.

Peterson, R. T. 2002. Peterson's field guides: eastern birds. Fifth Edition. Houghton Mifflin Company, Boston, Massachusetts, USA.

Spector, D. A. 1992. Wood-warbler song systems: review of Paruline singing behaviors. Current Ornithology 9:199–238.

The Wilson Journal of Ornithology 120(2):404–407, 2008

Substrate and Vegetation Selection by Nesting Piping Plovers

Jonathan B. Cohen,[1,3] Elizabeth H. Wunker,[2] and James D. Fraser[1]

ABSTRACT.—We studied substrate composition and vegetation cover at Piping Plover (*Charadrius melodus*) nests and paired random plots on New York beaches that had been widened by renourishment (deposition of dredged sand). Most nests (59.4%, $n = 32$) were in unvegetated plots, mean ± SE vegetative cover around nests was 7.5 ± 1.7%, and all plovers nested in <47% cover. Most nests (59.4%) were on pure sand and mean coarse grain cover (pebble and cobble-sized objects) on nest plots was 9.1 ± 2.6%. Nest plots were more likely to be vegetated than paired random plots. Coarse substrate also was of high relative importance in distinguishing nests and random plots. Beach management projects can reduce sparse vegetation and coarse substrate, which may affect Piping Plover nest site selection. *Received 9 December 2006. Accepted 1 August 2007.*

Piping Plovers (*Charadrius melodus*) selecting nest sites on Atlantic Coast beaches must balance the risks of tidal flooding and egg predation (Burger 1987). They scrape nests in bare or sparsely-vegetated sand, gravel, or shell substrates on beaches and interdune areas, at times adjacent to vegetation clumps, and rely on camouflage and an unobstructed view of their surroundings to avoid predation (Haig and Elliot-Smith 2004). They may nest close to large objects such as stones or logs (Haig and Elliot-Smith 2004), which may serve as windbreaks or nest markers (Warnock et al. 2002).

Atlantic Coast beaches often are altered by people who widen them (beach renourishment), build dunes, and plant vegetation (USDI 1996). These alterations are intended to protect human property (Finkl et al. 1988), but also may affect shorebird habitat. Plantings that lead to high stem densities may preclude shorebird nesting, and substrate or cover modifications may affect nest distribution and susceptibility to predation, weather, and flooding. Reducing the negative impacts of beach projects on Piping Plovers depends on understanding landscape traits that affect nest site selection.

We studied Piping Plover nest site selection on renourished beaches in New York in 2004 at sites where future renourishment was planned. Our objective was to learn if Piping Plover nest sites differed from nearby random sites in vegetative cover, coarse materials in the substrate, and number of large objects such as stones and woody debris.

METHODS

Study Area.—We studied Piping Plovers on Westhampton Island (40° 46′ N, 72° 43′ W), Long Island, New York, from March to August 2004. Our site consisted of a 6-km long ocean beach on the western end of the island and 3-km long ocean beach on the east end. The two sites were 15 km apart. The habitat contained several parallel cover type zones elongated east to west: ocean intertidal zone, bare backshore, sparsely vegetated backshore/dune, densely vegetated backshore/dune, and human land use. The U.S. Army Corps of Engineers renourished the western beach in winter 2000/2001 and 50% of the eastern beach in winter 2003/2004.

Field Methods.—We estimated substrate composition and vegetation cover around each nest in the first week of incubation using 1 × 1 m sampling quadrats with 36 grid intersections. We placed quadrats over nests with one side parallel to the shore and the nest under the central grid square. We recorded the presence of sand (rock grains <2 mm), pebble (2–64 mm), cobble (>64 mm), small shells (<2 mm), medium shells (2–64 mm), large shells (>64 mm), small dead wood (<64 mm), large dead wood (>64 mm), beach grass or other plant species (if a stem was emerging from the substrate at the intersection), and other material (such as wrack or debris) under each

[1] Department of Fisheries and Wildlife Sciences, Virginia Tech, Blacksburg, VA 24061, USA.

[2] Department of Environmental Studies, Warren Wilson College, Asheville, NC 28815, USA.

[3] Corresponding author; e-mail: jocohen1@vt.edu

TABLE 1. Characteristics at Piping Plover nests and random sites, Westhampton Island, New York, 2004 (n = 32, 1-m^2 nest and paired random plots within 50 m).

	Vegetation				Coarse grains				
	Cover (%)				Cover (%)				
Plot type	$\bar{x}$	SE	Max	Plots in[a] >5% cover	$\bar{x}$	SE	Max	Plots in[a] >5% cover	Plots near[b] ≥ 1 large object
Nest	7.6	1.7	45.7	0.41	9.1	2.6	55.6	0.41	0.28
Random	4.4	1.9	48.6	0.19	5.5	2.2	47.2	0.22	0.16

[a] Mean of the index used in our nest site selection model (0 = < 5% cover, 1 = 5–~100% cover).
[b] Mean of the large objects (rock, shell, wood >64 mm in at least one dimension) index used in our nest site selection model (0 = no large objects, 1 = ≥ 1 large object). Where large objects were present, counts ranged from 1 to 5.

grid intersection. We recorded the total number of large (>64 mm) objects within the quadrat, regardless of whether they were under an intersection.

We sampled a paired site at a randomly generated bearing (0–360°) and distance (1–50 m) from each nest. If we encountered an unsuitable cover type while walking from a nest to its paired point, we turned at a right angle and continued walking. If more than one right angle directed us into potential habitat, we flipped a coin to decide which way to turn.

Data Analyses.—We calculated percent vegetative cover as the number of grid points over an emerging plant/total grid points. We calculated percent cover of each substrate class as the total grid points over that class/total grid points without plants. We modeled selection of nest versus random plots using matched-pair logistic regression (Hosmer and Lemeshow 1998). We evaluated the global model fit using residual and influence plots (Hosmer and Lemeshow 1998). The data were too sparse for logistic regression at high levels of vegetative and coarse grain cover, and number of large objects. Therefore, we created categorical indices where 0 indicated <5% cover and 1 indicated 5–100% cover. Plots with ≥5% cover had at least two stems or coarse grains within the grid, and the 5% cutoff yielded adequate cell sizes for model fitting. We defined a large object index where 0 indicated no large objects and 1 indicated ≥one large object.

We performed regression analyses of all possible subsets, and identified the most parsimonious models using corrected Akaike's Information Criteria (AIC_c) and related information-theoretic criteria (Burnham and Anderson 2002). We inferred the importance of the explanatory variables' effects using model-averaged unconditional 95% confidence intervals (Burnham and Anderson 2002), and a relative importance (R_i) index (Burnham and Anderson 2002).

RESULTS

We collected data on 32 first nest attempts. Most nest and random plots were unvegetated,

TABLE 2. Piping Plover nest site selection model variables and information-theoretic criteria for all possible subsets of matched-pairs logistic regression models, Westhampton Island, New York, 2004 (n = 32, 1-m^2 nest and paired random plots within 50 m).

Variables in model	Number of parameters	AIC_c[a]	ΔAIC_c[b]	ω_i[c]	Model likelihood[d]
In vegetation (y/n), on coarse substrate (y/n)	2	38.883	0.000	0.568	1.000
In vegetation (y/n), on coarse substrate (y/n), large objects (y/n)	3	40.560	2.157	0.193	0.340
In vegetation (y/n), large objects (y/n)	2	41.424	3.984	0.077	0.136
In vegetation (y/n)	1	41.670	4.211	0.069	0.122
On coarse substrate (y/n)	1	42.640	5.531	0.036	0.063
Null	1	43.587	6.187	0.026	0.045
Large objects (y/n)	1	44.494	6.829	0.019	0.033
On coarse substrate (y/n), large objects (y/n)	2	45.130	7.578	0.013	0.023

[a] Corrected Akaike's Information Criterion.
[b] Difference between the AIC_c of a particular model and that of the best model.
[c] Model likelihood/Σlikelihood of all models.
[d] $e^{(-0.5 \times \Delta AIC_c)}$.

TABLE 3. Model-averaged effects of vegetation cover, coarse grain cover, and number of large objects on Piping Plover nest site selection (n = 32, 1-m^2 nest and paired random plots within 50 m), Westhampton Island, Long Island, New York, 2004.

Variable	Estimate	SE	95% Lower	CL Upper	R_i[a]
Vegetation cover > 5%	1.749[b]	0.820	0.141	3.356	0.907
Coarse grain cover > 5%	1.364	0.734	−0.074	2.802	0.809
Large objects present	0.175	0.263	−0.340	0.690	0.302

[a] Relative importance of variable = $\Sigma\omega_i$ of all models containing the variable.
[b] Significant effect (unconditional confidence intervals do not contain 0).

and most were on pure sand that contained no large objects (Table 1). Three of the eight models we tested had some support (model likelihood >0.125, Table 2). Nest plots were more likely to be vegetated than random plots based on model-averaged statistics using all eight models (Table 3). Percent cover by coarse grains was of high relative importance (Table 3), providing some evidence that plovers were more likely to nest in coarse substrates than in pure sand.

DISCUSSION

All Piping Plover nests in our study were in <50% cover with most on bare ground, but they occurred in vegetation more often than expected based on its availability. Apparent selection of vegetated nest sites may result if plovers nest near vegetated upland zones away from the water line to avoid flooding (Burger 1987, Espie et al. 1996). Average cover around nests in our study was less than in Maryland and Virginia (average 11%, range 9–16%; Patterson 1991) and Massachusetts (15.2 ± 23.6%; MacIvor 1990). Average cover at random points in Massachusetts was twice as high as in our study (8.7 ± 16%; MacIvor 1990) suggesting that vegetation was less available in our study area than in Massachusetts.

Plant loss due to recent renourishment (Looney and Gibson 1993) at our site may have explained why vegetation was relatively sparse. Nests in vegetation can experience more predation than those in the open (Prindiville Gaines and Ryan 1988, Espie et al. 1996). Thus, renourishment may benefit Piping Plovers by suppressing vegetation. However, renourishment often is followed by beach grass (*Ammophila* spp.) planting (French 2001) with initial ground cover ranging from 3 to 25%. Once beach grass becomes dense, it may have to be thinned each growing season because it can fully recover within 1 year of thinning (U.S. Army Corps of Engineers 1967).

Piping Plovers in Massachusetts (Jones 1997) and New Jersey (Burger 1987) selected territories with mixed substrate. The prevalence of nests in pure sand in our study may have been related to birds nesting away from the water, near the sandy dune. Coarse substrate may also not have been widely available; percent cover in random plots was approximately half of that at random sites in Massachusetts in the late 1980s (~11%; MacIvor 1990). This may also be a result of recent renourishment, which often creates fine-grained beaches (Atlantic States Marine Fisheries Council 2002). Coarse substrate was associated with high hatching success in North Dakota, most likely through camouflage of adults and eggs (Prindiville Gaines and Ryan 1992). Thus, reduced availability of pebbles and cobble may be a negative consequence of renourishment that could be mitigated by replacement of coarse grains.

ACKNOWLEDGMENTS

The U.S. Army Corps of Engineers, New York District, funded this research. The U.S. Fish and Wildlife Service, Long Island Field Office and Region 5 Office; New York Department of Environmental Protection; Suffolk County Parks; Town of Southampton; villages of West Hampton Dunes and Westhampton Beach, New York; and the Long Island Chapter of The Nature Conservancy provided logistical support. Field data were collected by Ellen Creveling, Bradley Pickens, and Dawn Wiley. D. H. Catlin and S. M. Karpanty reviewed the manuscript.

LITERATURE CITED

Atlantic States Marine Fisheries Council. 2002. Beach nourishment: a review of the biological and physical impacts. ASMFC Habitat Management Series # 7. Atlantic States Marine Fisheries Council. Washington, D.C., USA.

Burger, J. 1987. Physical and social determinants of nest-site selection in Piping Plover in New Jersey. Condor 89:811–819.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, USA.

Espie, R. H. M., R. M. Brigham, and P. C. James. 1996. Habitat selection and clutch fate of Piping Plovers (*Charadrius melodus*) breeding at Lake Diefenbaker, Saskatchewan. Canadian Journal of Zoology. 74:1069–1075.

Finkl Jr., C. F, J. Walker, and I. Watson. 1988. Shoreline erosion: management case history from southeast Florida. Ocean Shoreline Management 11:129–144.

French, P. W. 2001. Coastal defences: processes, problems, and solution. Routledge, London, United Kingdom.

Haig, S. M. and E. Elliott-Smith. 2004. Piping Plover (*Charadrius melodus*). The birds of North America. Number 2.

Hosmer, D. and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, USA.

Jones, L. K. 1997. Piping Plover habitat selection, home range and reproductive success at Cape Cod National Seashore, Massachusetts. Thesis. University of Massachusetts, Amherst, USA.

Looney, P. B. and D. J. Gibson. 1993. Vegetation monitoring related to beach renourishment of the Gulf Islands National Seashore, Perdido Key, Florida. Pages 226–241 *in* Coastal Zone 1993: Proceedings of the Eighth Symposium on coastal and ocean management (O. T. Magoon, W. S. Wilson, H. Converse, and L. T. Tobin, Editors). American Society of Civil Engineers, Reston, Virginia, USA.

MacIvor, L. H. 1990. Population dynamics, breeding ecology, and management of Piping Plovers on outer Cape Cod, Massachusetts. Thesis. University of Massachusetts, Amherst, USA.

Patterson, M. E., J. D. Fraser, and J. W. Roggenbuck. 1991. Factors affecting Piping Plover productivity on Assateague Island. Journal of Wildlife Management 55:526–531.

Prindiville Gaines, E. M. and M. R. Ryan. 1988. Piping Plover habitat use and reproductive success in North Dakota. Journal of Wildlife Management 52:266–273.

U.S. Army Corps of Engineers. 1967. Dune stabilization with vegetation on the Outer Banks of North Carolina. Technical Memorandum 22. Department of the Army, Corps of Engineers, U.S. Army Coastal Engineering Research Center, Washington, D.C., USA.

U.S. Department of Interior (USDI). 1996. Piping Plover (*Charadrius melodus*), Atlantic Coast Population. Revised Recovery Plan. USDI, Fish and Wildlife Service, Hadley, Massachusetts, USA.

Warnock, N., C. Elihick, and M. A. Rubeja. 2002. Shorebirds in the marine environment. *In* Shorebirds. Breeding behavior and populations (E. A. Schreiber and J. Burger, Editors). CRC Press, Boca Raton, Florida. USA.

The Wilson Journal of Ornithology 120(2):407–409, 2008

Nest Site Selection by a Male Black-capped Vireo

Andrew J. Campomizzi,[1,2] Shannon L. Farrell,[1] and Jerrod A. Butcher[1]

ABSTRACT.—We observed a male Black-capped Vireo (*Vireo atricapilla*) exhibiting nest site selection in east-central Texas. The paired male was observed to deconstruct the nest the female was assembling. To our knowledge, male nest site selection has not been observed and reported in the literature for vireos. *Received 11 December 2006. Accepted 6 September 2007.*

It is not uncommon for male passerines to begin building nests before they form pair bonds (James 1978, Collias and Collias 1984). Cooperative and male-initiated nest-building behaviors are related to pair bonding, parental quality, and the ability of males to invest in reproduction (Collias and Collias 1984, Hoi et al. 1996, Soler et al. 1998). Nest building by males prior to pairing has been observed in several vireo species including Plumbeous Vireo (*Vireo plumbeus*) (DeMarco et al. 2000), Bell's Vireo (*V. bellii*) (Brown 1993), and Yellow-throated Vireo (*V. flavifrons*) (James 1978, Rodewald and James 1996). James (1978) observed male Blue-headed Vireos (*V. solitarius*) building nests before pairing. James (1978) also noted that commencement of paired nest building occurred soon after pairing and hypothesized that males were selecting nest sites. Graber (1961) ob-

[1] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA.

[2] Corresponding author; e-mail: acampomizzi@neo.tamu.edu

served that male Black-capped Vireos (*V. atricapilla*) began building nests before pairing. She reported that, after pairing, a nest would be built by the pair and concluded it was the female that selected the nest site. We observed a male Black-capped Vireo exhibiting nest site selection in April 2006. We also observed the male deconstructing the nest the female was assembling. To our knowledge, these behaviors have not been observed and reported for vireos.

OBSERVATIONS

We conducted nest searching as one component of research to monitor occupancy and population trends of Black-capped Vireos on private land in Coryell and Hamilton counties in east-central Texas. We monitored 17 pairs of Black-capped Vireos for ~864 hrs from 16 March to 31 July 2006. We monitored each nesting pair 2 days per week.

We first observed the male Black-capped Vireo on 17 April as it carried nest building material twice to a fork in a branch of a shin oak (*Quercus sinuata*) ~0.5 m from a large downed Ashe juniper (*Juniperus ashei*). The male was observed for >3 hrs and a female was not detected. We observed the male singing within 20 m of this first nest (nest A) and up to 250 m distant. Nest A consisted of strands of webbing in a slightly cup-shaped platform typical of a partially built vireo nest. We observed the male within 5 m of nest A on 20 April. Nest A was unchanged and a female was not detected. We observed the male for 3 hrs singing within 20 m of nest A and up to 250 m distant on 24 April. We did not observe a female on 24 April and the condition of the nest A was unchanged.

We observed a female Black-capped Vireo with the male on 27 April. We observed the male singing within 10 m of the female at 0920 hrs. The female carried nesting material to nest A at 0935 hrs which was ~15% built. At 1000 hrs the female carried nesting material north to a different location where nest B was later found. The female carried nesting material to nest B again at 1115 hrs. While the female was arranging nesting material at nest B, the male landed next to her and the female flushed from the nest. The male pulled material from nest B and flew in the direction of nest A. Nest B was ~10% built at that time. We observed the male and female at nest A at 1130 hrs. Between 1130 and 1200 hrs the male flew to nest A without nesting material and perched ~1 m from the nest five times. During the same period, the female carried nesting material to nest A twice.

Nest A was completed on 1 May and we observed the male singing within 10 m of the nest. The condition of nest B was unchanged from 27 April. Nest A was empty on 4 May and still in completed condition. We observed four Black-capped Vireo eggs and one Brown-headed Cowbird (*Molothrus ater*) egg in nest A on 8 May. Nest A was empty and undamaged on 11 May. We observed this pair for approximately 29 hrs throughout the breeding season. During this time, the pair built and laid eggs in three additional nests. We did not locate any other breeding pairs of Black-capped Vireos within ~1.5 km of their territory.

DISCUSSION

Our observations suggest the male Black-capped Vireo preferred one nest over another, selecting it while the female was actively building both nests. Our observations may reflect behaviors involved in the process of nest site selection. It is possible the male began building both nests and then selected one. It is not uncommon for male Black-capped Vireos to begin building nest rims prior to pairing (Grzybowski 1995). These beginning nests are often displayed to females as part of courtship and may subsequently serve as an active nest with approval of the female. We have observed Black-capped Vireo pairs deconstructing old nests for material to be used in new nests. Bent (1950) and Nolan (1960) described aggressive interactions between male and female vireos during courtship and nest building. However, we were unable to find reports in the literature of males selecting nests sites to the contrary of the female's choice or males deconstructing a nest being built by a female by actively removing nest material. It is possible this behavior occurs occasionally but is not observed or reported. Grzybowski (1990) reported that Black-capped Vireos often nest in aggregations and smaller aggregations contain a greater proportion of second-year males. We did not detect other Black-capped Vireos nesting within 1.5 km of this pair. We did not ascertain the age of these birds and speculate the male may have been in his second-year;

the behavior we observed may be the result of a lack of breeding experience or inequality in experience between the male and female.

It is difficult to draw any conclusions concerning male nest site selection in Black-capped Vireos based on the observations of one pair. We suggest that researchers consider this behavior to document the frequency of male nest site selection. If male nest site selection is not uncommon, there may be opportunities for researchers to examine differences in male initiated nests versus female initiated nests including nest success, nest site characteristics, and initiation dates.

ACKNOWLEDGMENTS

Funding was provided by a grant from the U.S. Department of Defense, Environmental Readiness Program. We thank the private land owners who allowed us to work on their properties, M. L. Morrison and R. N. Wilkins for guidance in our research and constructive comments on this manuscript, and our field technicians for their efforts.

LITERATURE CITED

Bent, A. C. 1950. Life histories of North American wagtails, shrikes, vireos and their allies. U.S. National Museum Bulletin Number 197.

Brown, B. T. 1993. Bell's Vireo (*Vireo bellii*). The birds of North America. Number 35.

Collias, N. E. and E. C. Collias. 1984. Mate selection and nest building. Pages 57–73 *in* Nest building and bird behavior. Princeton University Press, Princeton, New Jersey, USA.

DeMarco, T. E., C. B. Goguen, D. R. Curson, and N. E. Mathews. 2000. Breeding behavior of the Plumbeous Vireo in New Mexico. Western North American Naturalist 60:394–402.

Graber, J. W. 1961. Distribution, habitat requirements, and life history of the Black-capped Vireo (*Vireo atricapilla*). Ecological Monographs 31:313–336.

Grzybowski, J. A. 1990. Population and nesting ecology of the Black-capped Vireo in Texas—1988–1989. USDI, Fish and Wildlife Service, Ecological Services, Arlington, Texas, USA.

Grzybowski, J. A. 1995. Black-capped Vireo (*Vireo atricapillus*). The birds of North America. Number 181.

Hoi, H., B. Schleicher, and F. Valera. 1996. Nest size variation and its importance for mate choice in Penduline Tits, *Remiz pendulinus*. Animal Behaviour 51:464–466.

James, R. D. 1978. Pairing and nest site selection in Solitary and Yellow-throated vireos with a description of a ritualized nesting display. Canadian Journal of Zoology 56:1153–1159.

Nolan, V. 1960. Breeding behavior of the Bell's Vireo in southern Indiana. Condor 62:225–244.

Rodewald, P. G. and R. D. James. 1996. Yellow-throated Vireo (*Vireo flavifrons*). The birds of North America. Number 247.

Soler, J. J., A. P. Møller, and M. Soler. 1998. Nest building, sexual selection and parental investment. Evolutionary Ecology 12:1153–1159.

The Wilson Journal of Ornithology 120(2):409–412, 2008

Nests of Black-throated Green Warblers in Tree Cavities

Douglas C. Tozer[1]

ABSTRACT.—Black-throated Green Warblers (*Dendroica virens*) typically place their nests within the dense foliage of a limb or in a branch fork against the trunk of a living conifer. I report four unusual nests from Algonquin Provincial Park, Ontario, Canada: three in feeding cavities of Pileated Woodpecker (*Dryocopus pileatus*) in snags (i.e., dead trees), and one in a sugar maple borer (*Glycobius speciosus*, Coleoptera: Cerambycidae) scar in a tree of declining health. These data are the first documentation of this species nesting within cavities and enhance our understanding of the importance of snags and trees in declining health for wildlife. *Received 15 February 2007. Accepted 20 September 2007.*

[1] Watershed Ecosystems Graduate Program, Environmental Science Centre, 1600 West Bank Drive, Trent University, Peterborough, ON K9J 7B8, Canada; e-mail: dtozer@trentu.ca

Black-throated Green Warblers (*Dendroica virens*) are common breeding birds in a variety of forest types ranging from mostly coniferous to predominantly deciduous across the southern half of Canada east of Alberta, and in parts of the eastern United States (Morse 1993). Throughout its range, the species is

FIG 1. Nests of Black-throated Green Warblers in Pileated Woodpecker feeding cavities (A–C) and in a sugar maple borer scar (D) in Algonquin Provincial Park, Ontario, Canada. Photographs taken in May or June 2006 while nests were active, except B (Oct 2006).

closely tied to conifers for nesting (Robichaud and Villard 1999) but, depending on geographical location and habitat, it may prefer either coniferous or deciduous substrates for foraging (Parrish 1995). The species normally selects a territory that contains groups of eastern hemlock (*Tsuga canadensis*) and other conifers (e.g., eastern white cedar [*Thuja occidentalis*] and white spruce [*Picea glauca*]) in forests dominated by sugar maple (*Acer saccharum*) in central Ontario (Crins 1987, Peck and James 1987); some territories contain only one or two canopy-sized conifers (Robichaud and Villard 1999) or none at all (Bent 1953). Even within territories that contain only a few conifers, it appears to prefer to place its nest in coniferous (83%) versus deciduous (17%) trees (n = 41 nests in Ontario; Peck and James 1987), typically within the dense foliage of a limb or in a branch fork against the trunk (Harrison 1975, 1979).

The objective of this paper is to describe four unusual nests of Black-throated Green Warblers that were built in cavities in trees. To my knowledge, no previous study has documented use of cavities for nesting by this species (e.g., Chapman 1907, Bent 1953, Morse 1993) and none of the records currently in the Ontario Nest Records Scheme mention use of cavities for nesting (n = 74 nests; Peck and James 1987; M. K. Peck, pers. comm.).

OBSERVATIONS

I conducted extensive nest searching between early-May and late-July 2006 in 22 sugar maple-dominated forest stands (15–40 ha each) scattered across the western portion (~3,500 km^2) of Algonquin Provincial Park, Nipissing District, Ontario, Canada (45° 37′ N, 78° 21′ W). The canopy of each stand was ~85% sugar maple with the remainder predominantly American beech (*Fagus grandifolia*), eastern hemlock, and yellow birch (*Betula alleghaniensis*). The stands were at different stages within the single-tree selection (Hunter 1990) harvest cycle (~25 years between cuts) or were uncut reference stands that had not been cut for 60 years.

I incidentally located six nests of Black-throated Green Warblers; four of these nests were unusual as three were at the bottom of Pileated Woodpecker (*Dryocopus pileatus*) feeding cavities in snags (i.e., dead trees; Fig. 1A–C) and the fourth was at the bottom of a sugar maple borer (*Glycobius speciosus*, Coleoptera: Cerambycidae) scar (Fig. 1D). The scar was healing, but had protruding bark at the bottom that supported and concealed the nest from below, above, and three-quarters of the sides (Fig. 1D) allowing the adults to enter the well-concealed nest through the remaining open quarter. The nests were in three tree species and were 1.5–4.5 m above the ground; one nest successfully fledged young, one was depredated by an unknown predator, and the fates of the others were unknown (Table 1). One nest was inactive when found, but the material, size, and structure of the cup matched the rest of the nests where adults were observed. There were at least five mature, canopy-sized eastern hemlocks within a 75-m radius of each of the four nests suggesting the absence of conifers (the favored nesting substrate) was not a factor influencing the birds to place their nests in cavities. One to four male Black-throated Green Warblers were on territory in each of the 22 stands, especially where eastern hemlocks provided a coniferous canopy component.

DISCUSSION

Previous reports have described unusual nesting locations for Black-throated Green Warblers. Three nests were in open areas: 0.2 m above ground in a small red cedar (*Juniperus virginiana*) in a reclaimed pasture (Bent 1953); in a barberry (*Berberis* spp.) ~100 m from the nearest forest (Brewster 1906); and well-concealed within a grapevine (*Vitis* spp.) "some distance from any woods" (Brown 1889:74). Two nests were at low heights in swampy forest: 0.3 m above ground in the stems of a skunk cabbage (*Symplocarpus foetidus*), catbriar (*Smilax rotundifolia*), and a dead bush (Bowdish 1906); and on the ground among ferns (Brewster 1895). The geographically isolated subspecies *D. v. waynei* of the southeastern United States coastal plain regularly nests at a variety of heights in cypress (*Taxodium* spp.), oak (*Quercus* spp.), and magnolia (*Magnolia* spp.) (Morse 1993).

TABLE 1. Nest site characteristics of Black-throated Green Warblers in Pileated Woodpecker feeding cavities and a sugar maple borer scar in Algonquin Provincial Park, Ontario, Canada.

Fig. 1[a]	Nest site	Tree species[b]	Nest height (m)	Tree height (m)	Diameter breast height (cm)	Decay class[c]	Years since last harvest[d]	Dates under observation	Contents	Nest fate
A	Feeding cavity	Bf	1.5	6.0	36	4	26.5	2–13 Jun	Known clutch size 2	Both young fledged
B	Feeding cavity	Be	1.7	3.7	38	5	>60	6 Oct	Unknown, inactive	Unknown
C	Feeding cavity	Mh	2.7	8.1	43	4	23.5	19–21 Jun	3 young; clutch size unknown	Depredated
D	Scar	Mh	4.5	20	32	n/a[e]	21.5	25 May	Unknown, female on nest	Unknown

[a] Corresponds to the letter in Figure 1.
[b] Bf = balsam fir (*Abies balsamea*), Be = American beech, Mh = sugar maple.
[c] Following OMNR (2000): 1 = recently dead, top intact, fine branching present; 2 = top intact, most fine branches fallen, greater than 50% coarse branches remain; 3 = top intact, less than 50% coarse branches remain; 4 = top broken, no coarse branches remain; 5 = stub only, top broken, height less than 6 m.
[d] Years since last harvest under single-tree selection.
[e] Alive but with declining health.

It is perhaps not surprising that this species, at least occasionally, nests in cavities. At least two other wood-warblers (Parulidae) that normally do not place their nests in cavities have been documented using them: Orange-crowned Warbler (*Vermivora celata*), which normally nests in well-concealed locations among ground detritus in small depressions or crevices and only occasionally builds elevated nests in dense vegetation (Sogge et al. 1994), has nested 3.2 m above ground in a natural cavity of a canyon maple (*Acer grandidentatum*) (Zyskowski 1993); and Common Yellowthroat (*Geothlypis trichas*), which normally nests on or up to 0.1 m above ground in thick vegetation (Guzy and Ritchison 1999), has nested 0.6 m above ground in a shoe that was hung on the side of a house (Brockway 1899). Cavity-use by nesting Black-throated Green Warblers may be a regular but infrequent occurrence.

Future research is warranted to identify the frequency and importance of cavity-nesting by Black-throated Green Warblers. It is not known if tree harvesting activities may or may not be influencing this little-known nesting behavior by reducing the number of snags and trees of declining health that might have served as cavity nesting sites.

ACKNOWLEDGMENTS

I thank Kris Vande Sompel and Peter Burke for finding three of the unusual nests, and Karla Falk, Meaghan Noad, Andrea Orr, Eleanor Proctor, Sonya Richmond, and Philip Wilson for help with monitoring. Kris Vande Sompel (Fig. 1A, C) and Peter Burke (Fig. 1D) provided photographs. Kristof Zyskowski, an anonymous reviewer, Ken Elliott in particular, Dawn Burke, Karla Falk, Erica Nol, Pat Tozer, and Ron Tozer provided helpful comments that improved earlier drafts of the mansucript. Keith Fletcher, Brad Steinberg, Paul Gelok, Andrew Trant, and the Algonquin Park Wildlife Research Station helped with logistics. Funding and in-kind support were provided by Algonquin Forestry Authority, Bancroft Minden Forest Co., Canadian Wildlife Service, Canadian Forest Service, Enhanced Forest Productivity Science Program, Mazinaw-Lanark Forest Inc., Natural Sciences and Engineering and Research Council of Canada, Ontario Ministry of Natural Resources, Ottawa Valley Forest Inc., Tembec Inc., Trent University, and Westwind Forest Stewardship.

LITERATURE CITED

Bent, A. C. 1953. Life histories of North American wood warblers. Part 1. U.S. National Museum Bulletin Number 203.

Bowdish, B. S. 1906. Some breeding warblers of Demarest, N.J. Auk 23:16–19.

Brewster, W. 1895. A ground nest of the Black-throated Green Warbler. Auk 12:184–185.

Brewster, W. 1906. The birds of the Cambridge region of Massachusetts. Memoirs of the Nuttall Ornithological Club 4:1–426.

Brockway, W. 1899. Odd nesting of Maryland Yellow-throat. Auk 16:360–361.

Brown, J. C. 1889. Unusual nesting site of *Dendroica virens*. Auk 6:74.

Chapman, F. M. 1907. The warblers of North America. D. Appleton, New York, USA.

Crins, W. J. 1987. Black-throated Green Warbler. Pages 382–383 *in* Atlas of the breeding birds of Ontario (M. Cadman, P. Eagles, and F. M. Helleiner, Compilers). University of Waterloo Press, Waterloo, Ontario, Canada.

Guzy, M. J. and G. Ritchison. 1999. Common Yellowthroat (*Geothlypis trichas*). The birds of North America. Number 448.

Harrison, H. H. 1975. A field guide to birds' nests: United States east of the Mississippi River. Peterson Field Guide Series. Houghton Mifflin, Boston, Massachusetts, USA.

Harrison, H. H. 1979. A field guide to western birds' nests: United States west of the Mississippi River. Peterson Field Guide Series. Houghton Mifflin, Boston, Massachusetts, USA.

Hunter, M. L. 1990. Wildlife, forests, and forestry. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Morse, D. H. 1993. Black-throated Green Warbler (*Dendroica virens*). The birds of North America. Number 55.

Ontario Ministry of Natural Resources [OMNR]. 2000. A silvicultural guide to managing southern Ontario forests. Ontario Ministry of Natural Resources. Queen's Printer, Ontario, Toronto, Canada.

Parrish, J. D. 1995. Experimental evidence for intrinsic microhabitat preferences in the Black-throated Green Warbler. Condor 97:935–943.

Peck, G. K. and R. D. James. 1987. Breeding birds of Ontario: nidiology and distribution. Volume 2. Passerines. Royal Ontario Museum, Toronto, Canada.

Robichaud, I. and M. Villard. 1999. Do Black-throated Green Warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. Condor 101:262–271.

Sogge, M. K., W. M. Gilbert, and C. van Riper III. 1994. Orange-crowned Warbler (*Vermivora celata*). The birds of North America. Number 101.

Zyskowski, K. 1993. Nest-site selection in Orange-crowned and Virginia's warblers in high-elevation forests of the Mogollen Rim (Arizona): variation in nest placement, phenology, and microclimate. Thesis. University of Arkansas, Fayetteville, USA.

The Wilson Journal of Ornithology 120(2):413–416, 2008

Nest and Fledglings of the Red-ruffed Fruitcrow (*Pyroderus scutatus*)

Mercival R. Francisco,[1,4] Paulo R. R. Oliveira Jr.,[2] and Vitor O. Lunardi[3]

ABSTRACT.—Information on the breeding behavior of the Red-ruffed Fruitcrow (*Pyroderus scutatus*) is scarce and restricted to the subspecies *P. s. granadensis* and *P. s. orenocensis*. We found the first nest of the nominate subspecies (*P. s. scutatus*) in an Atlantic Forest area in southeastern Brazil on 28 November 2004. The nest contained two nestlings and was built on a horizontal fork, 16.7 m above ground. It was cup-shaped with a substantial base composed of twigs: outside diameter 38 cm, cup diameter 16.5 cm, outside height 11.3 cm, and inside height 5 cm. The nestlings were thickly covered with brownish down. Only one unknown gender adult visited the nest. Although locally endangered, the breeding cycle of this species remains poorly known. *Received 10 February 2007. Accepted 12 September 2007.*

The cotingas comprise a diverse group of birds endemic to the Neotropics (Snow 1982). They inhabit tropical and subtropical forests, and most species are arboreal. These birds are of great interest because different species exhibit unusual courtship displays while others have bright plumage or bizarre ornaments. However, information on their breeding biology is scarce (Snow 1982, Ridgely and Tudor 1994, Sick 1997).

The Red-ruffed Fruitcrow (*Pyroderus scutatus*) is a large cotingid which inhabits humid and montane forests, forest borders, and locally somewhat drier regions. Five subspecies are recognized and our paper focuses on the nominate subspecies (from southeastern Brazil, eastern Paraguay, and northeastern Argentina) (Snow 2004).

Information on the breeding behavior of the Red-ruffed Fruitcrow is scarce and restricted to the subspecies *P. s. granadensis* and *P. s. orenocensis*. Nests described for *P. s. granadensis* in Colombia are open shallow cups with the base made mainly of twigs and the cup composed exclusively of the fronds of ferns, placed 5–8 m above ground in slender tree branches (Serrano 1994, Snow 2004). The objectives of our paper are to: (1) describe the nest of the nominate subspecies, *P. s. scutatus*, from southeastern Brazil, and (2) describe the nestlings.

OBSERVATIONS

The nest was found on 28 November 2004 at Carlos Botelho State Park, São Paulo State, southeastern Brazil (24° 04′ 14.6″ S, 47° 57′ 34.3″ W, altitude 851 m). This park contains 37,664 ha of coastal Atlantic Forest at an altitude of 22 to 1,000 m above sea level. Annual rainfall can exceed 160 cm in higher elevations.

The nest contained two nestlings and was in a primary forest area where the canopy reached 30–35 m. It was built in a honey wood tree (*Alchornea triplinervia*, Euphorbiaceae), 18 m in height at an overhanging branch, 4 m from the trunk and 16.7 m above ground. The nest was in a horizontal fork with branches ~5 cm in diameter. Ferns were abundant at the tree crown making the nest almost undetectable from the ground, as well as from the top of the tree. The nest was cup-shaped with a substantial base composed of twigs and the cup was thinly built with dry stripped ferns (Fig. 1). The measurements of the nest were: outside diameter 38 cm, cup diameter 16.5 cm, outside height 11.3 cm, and inside height 5 cm. The nestlings were thickly covered with brownish down, which was concentrated on their heads and hung over their eyes, that were already open. The bill and gape

[1] Universidade Federal de São Carlos, Campus de Sorocaba, CEP 18043-970, Caixa Postal 3031, Sorocaba, SP, Brazil.

[2] Universidade Estadual Paulista, Campus de Assis, Departamento de Ciências Biológicas, Laboratório de Comportamento de Vertebrados, Avenue Dom Antonio, 2100, CEP 19806-900, Assis, SP, Brazil.

[3] Universidade de Brasília, Campus Universitário Darcy Ribeiro, ICC-Sul, Instituto de Ciências Biológicas, Programa de Pós-Graduação em Ecologia, CEP 70910-900, Brasília, DF, Brazil.

[4] Corresponding author; e-mail: mercival@power.ufscar.br

FIG. 1. Nest and young Red-ruffed Fruitcrow in Carlos Botelho State Park, SP, Brazil (photograph by M. R. Francisco).

were yellow, and the throat was poorly feathered with a remarkable pinkish skin. The primary pin feathers were visible, but were broken only at the tip, suggesting the nestlings were fairly young. They were similar in size and were sedentary, not moving or making sounds when handled. An adult repeatedly approached the nest to within 1.5 to 2 m while the nest was being examined.

We conducted 12 hrs of focal observations from 0530 to 1730 hrs (UTC-3) on 1 December 2004 during which only one unknown gender adult (identified by a broken feather in its tail) visited the nest 40 times. The nestlings were not brooded after being fed except when it was raining. The adult spent 26 and 114 min at the nest, respectively, during two heavy storms. We do not know if the adult brooded the nestlings at night. Visits were 9–192 sec in length (46.52 ± 46.09 sec, $n = 27$) (mean ± SD) when it was not raining and the time between visits averaged 13.71 ± 9.9 min (range: 4–43 min, $n = 35$). The adult perched ~10–15 m from the nest before provisioning the young and carefully checked the surrounding area for 10–30 sec, possibly to avoid attracting potential predators to the nest. Routes taken by the adult to and from the nest varied. Upon leaving the nest, the adult frequently flew directly to the ground, apparently to capture insects. The adult was observed carrying large insects in its bill in 14 of the 40 visits. Regurgitated seeds of palmito (*Euterpe edulis* ($n = 1$) and *Virola oleifera* ($n = 3$) were found on the top of the branch on which the nest was placed. No fecal material was found near the nest, suggesting the adult removed fecal sacs. The parent was observed chasing

another adult Red-ruffed Fruitcrow that had approached the nest to within 5–6 m on five occasions.

DISCUSSION

Many large and medium-sized cotingas, such as species in the genera *Procnias*, *Lipaugus*, *Xipholena*, *Perissocephalus*, *Cephalopterus*, and *Carpodectes* build extraordinarily small and flimsy open nests, usually supported by twigs or small branches. Some species are known to use lichens, mosses, and similar materials for camouflage (Snow 1982, 2004; Sánchez 2002). The nest of the Red-ruffed Fruitcrow we observed was quite large and did not present materials for camouflage. However, it was hidden in the middle of ferns on an inaccessible branch. Chasing potential predators appears to be a method of nest defense in this species as T. K. Salmon (Snow 1982) and Serrano (1994) observed Red-ruffed Fruitcrows leaving the nests to chase hawks that approached their territories. A base composed of twigs and the cup built with stripped ferns was also observed for *P. s. granadensis* (Serrano 1994). Snow (2004) noted that Red-ruffed Fruitcrow nests are shallow cups that allow light to pass through, but the base of the nest we observed was bulky and substantial. We observed two nestlings, but clutch sizes in *P. s. granadensis* were invariably one (n = 6 nests) (Serrano 1994, Snow 2004).

The nest we observed was found during the rainy season in southeastern Brazil and coincided with the peak of ripening of palmito fruits in the area. Four to five fruiting palmito trees could be seen from the nest, as it was the most abundant tree with fruit at that location. The presence of a regurgitated palmito seed close to the nest suggests the young were fed this fruit. The relationship between nesting activities of the Red-ruffed Fruitcrow and availability of palmito fruits should be examined as entire populations of this tree have been lost to palm heart harvesting (Galetti and Aleixo 1998). In some areas, *P. scutatus* are only seen during the fruiting period of *Euterpe edulis* (Galetti et al. 1999).

The Red-ruffed Fruitcrow is not globally threatened, but *P. s. scutatus* is listed as endangered in many Brazilian states including Rio Grande do Sul, São Paulo, Minas Gerais, and Rio de Janeiro. Many populations of this species have declined, presumably due to habitat fragmentation and destruction of the Atlantic Forest ecosystem (Willis 1979, Ribon et al. 2003, Snow 2004). Only 7.5% of the original 1 million km^2 area of Atlantic Forest remains distributed in several small and disconnected fragments, and a few large forest tracts (Myers et al. 2000). Large frugivores, such as the Red-ruffed Fruitcrow are among the first species that disappear in small woodlots (Willis 1979, Ribon et al. 2003). The data in this paper provide a starting point for understanding the breeding beahvior of *P. s. scutatus* and may be useful in the future conservation of the species.

ACKNOWLEDGMENTS

We are grateful to L. F. Silveira, H. L. Gibbs, César Sánchez, and an anonymous referee for important comments on early versions of this manuscript. We also thank Instituto Florestal do Estado de São Paulo (IF) for permits for field work at Carlos Botelho State Park.

LITERATURE CITED

Galetti, M. and A. Aleixo. 1998. Effects of palm heart harvesting on frugivores in the Atlantic Forest of Brazil. Journal of Applied Ecology 35:286–293.

Galetti, M., V. B. Zipparro, and P. C. Morellato. 1999. Fruiting phenology and frugivory on the palm *Euterpe edulis* in a lowland Atlantic Forest of Brazil. Ecotropica 5:115–122.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Ribon, R., J. E. Simon, and G. T. Mattos. 2003. Bird extinctions in Atlantic Forest fragments of the Viçosa region, southeastern Brazil. Conservation Biology 17:1827–1839.

Ridgely, R. S. and G. Tudor. 1994. The birds of South America. Volume 2. University of Texas Press, Austin, USA.

Sánchez, C. 2002. Nest, egg, and nesting biology of the Snowy Cotinga (*Carpodectes nitidus*). Wilson Bulletin 114:517–519.

Serrano, V. H. 1994. Generalidades sobre la selección de habitat, el ciclo reproductivo y el sistema lek de apareamiento de *Pyroderus scutatus* (toro de monte). Pages 343–355 *in* Ucumari: un caso típico de la diversidad biótica Andina (J. O. Rangel, Editor). Carder Corporación Autónoma and Universidad Nacional de Colombia, Cali.

Sick, H. 1997. Ornitologia Brasileira. Editora Nova Fronteira, Rio de Janeiro, Brazil.

Snow, D. 1982. The cotingas: bellbirds, umbrellabirds

and other species. Cornell University Press, Ithaca, New York, USA.

Snow, D. B. 2004. Family Cotingidae (cotingas). Pages 32–108 *in* Handbook of the birds of the world. Volume 9. Cotingas to pipits and wagtails (J. del Hoyo, A. Elliott, and D. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Willis, E. O. 1979. The composition of avian communities in remanescent woodlots in southern Brazil. Papéis Avulsos de Zoologia 33:1–25.

The Wilson Journal of Ornithology 120(2):416–418, 2008

Palila (*Loxioides bailleui*) Fledgling Fed by Hawai'i 'Amakihi (*Hemignathus virens*)

Chris Farmer,[1,4] Bridget A. Frederick,[1,3] Paul C. Banko,[2] Robert M. Stephens,[1] and Carter W. Snow[1]

ABSTRACT.—We observed an adult male Hawai'i 'Amakihi (*Hemignathus virens*) repeatedly feed a fledgling Palila (*Loxioides bailleui*). We observed 16–19 food provisions during 14 hrs of observation between 21 and 29 June 2006. The presumed biological parents were frequently seen nearby, but adult Palila were not observed feeding the fledgling. *Received 28 April 2007. Accepted 26 July 2007.*

Interspecific parental care among nonbrood parasitic birds is rare and appears to have no ultimate, evolutionary benefits (Shy 1982, McNair and Duyck 1991, Yoerg and O'Halloran 1991, Lozano and Lemon 1998, Dróżdż et al. 2004). Shy (1982) proposed numerous possible proximate causes for such behavior. These can be encompassed by a few, underlying ultimate causes such as the high cost of ignoring one's own offspring, adult response to a super-normal juvenile stimulus or gaining experience in chick-rearing.

Interspecific feeding within the Hawaiian honeycreepers (Drepanidinae: Fringillidae) is unknown. Palila (*Loxioides bailleui*) of all age classes primarily consume the unhardened seeds of the māmane (*Sophora chrysophylla*) and have relatively low reproductive capacity (van Riper 1980, Banko et al. 2002). Palila typically have one brood per year (mean = 2 eggs), in part because fledglings do not become independent until they are 3–4 months of age (Miller 1998). Conversely, Hawai'i 'Amakihi (*Hemignathus virens*; hereafter 'Amakihi) are generalists that typically feed on arthropods and nectar, have two clutches per year (mean = 2.5 eggs per clutch), and provide parental care for 2–3 months (Lindsey et al. 1998). The dissimilar natural histories of the two species have resulted in considerable differences in their abundance and distribution. Approximately 2,000–3,000 Palila remain in the subalpine māmane and naio (*Myoporum sandwicense*) forest on the western slope of Mauna Kea on the island of Hawai'i (Banko et al. 2002, Johnson et al. 2006). In contrast, 'Amakihi are abundant throughout a wide range of habitats and elevations in Hawai'i (Scott et al. 1986, Lindsey et al. 1998). The objective of our paper is to document interspecific provisioning between these two Drepanidinae species.

METHODS

Our observations occurred at ~2,350 m elevation on the northern slope of Mauna Kea Volcano, Hawai'i Island (19° 53′ N, 155° 26′ W). This habitat is dry, open woodland dominated by māmane with scattered naio and an exotic grass understory (e.g., *Dactylis glom-*

[1] U.S. Geological Survey, Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo/PACRC, Kīlauea Field Station, P. O. Box 44, Hawai'i National Park, HI 96718, USA.

[2] U.S. Geological Survey, Pacific Island Ecosystems Research Center, Kīlauea Field Station, P. O. Box 44, Hawai'i National Park, HI 96718, USA.

[3] Current address: P. O. Box 6712, Hilo, HI 96720, USA.

[4] Corresponding author; e-mail: chris_farmer@usgs.gov

erata, *Holcus lanatus*, *Anthoxanthum odoratum*, and *Poa pratensis*). A small population of Palila has been created at this site through translocations from the main population on the western slope of Mauna Kea and releases of captive-reared birds by the Zoological Society of San Diego. The population consisted of ~30 Palila at the time of our observations (21–29 Jun 2006); nearly all were marked with colored plastic and U.S. Geological Survey aluminum leg bands. The 'Amakihi is the most abundant native or alien passerine found in this habitat (Scott et al. 1986; USGS, unpubl. data).

Ornithologists familiar with the local bird community used 8 × 32 binoculars to observe the birds, usually within a distance of 10 m. Behavioral observations were usually made by 1–2 observers, although on 29 June four people watched the fledgling-adult interactions.

OBSERVATIONS

Our observations were of an adult male 'Amakihi feeding a fledgling Palila, apparently providing the fledgling with most of its food during a 9-day period in June 2006. Two unbanded Palila fledglings of approximately the same age (25–28 days after hatch) were seen 0.3 m apart in a naio tree on 15 June 2006. A banded adult male and female Palila flew into the tree and fed at least one fledgling, which we assume was their offspring. This pair was engaged with their third reproductive attempt of the season at the time of our observations, having produced a 4-month-old fledgling prior to the 1-month-old fledgling and its sibling described above. The female was incubating an egg (later found to be infertile) in a third nest, 200 m from the fledgling, which was eventually abandoned, and the pair subsequently started, but did not finish, a fourth nest. We witnessed a banded (aluminum band only) adult male 'Amakihi feeding a Palila fledgling on 21 June. The fledgling chased after the 'Amakihi, which twice placed its bill down the fledgling's throat in a manner suggesting food regurgitation.

We banded a Palila fledgling on 22 June that we presumed to be the one that was fed by the 'Amakihi, based on its subsequent interspecific association. The fledgling weighed 29 g, 6 g less than the average hatch-year weight, but its subcutaneous furcular fat (score = 3) was relatively high for its age class (mode = 2; n = 357; USGS, unpubl. data).

We relocated the Palila fledgling in the same area on 27 June and observed it repeatedly begging and being fed by a banded male 'Amakihi. We saw two feedings and heard seven others, based on changes in the begging calls, over 5 hrs of observation. The Palila fledgling pursued the 'Amakihi through the trees, ignoring several nearby Palila adults, including a male that was the presumptive father. Similar behavior was observed during 3 hrs on 28 June when we saw the fledgling being fed by a banded male 'Amakihi at least four times and heard a possible fifth feeding. The fledgling fed independently upon the flowers of a native mint (*Stenogyne rugosa*) and young leaves of māmane and naio, but was not observed eating māmane pods. The Palila fledgling was last seen on 29 June when it was fed up to three times over 5 hrs of observation. We observed 16–19 feedings in 14 hrs (~1.1 provisionings/hr) over 9 days during which the juvenile began its third week after fledging.

DISCUSSION

Our repeated observations of an adult male 'Amakihi feeding a fledgling Palila are unique for the Drepanidinae and are the only record of feeding interactions between Palila and any other bird species in 30 years of Palila research (Banko et al. 2002). We believe that only one 'Amakihi fed the Palila fledgling, because the bird we observed was banded with an aluminum band, his appearance was consistent among observations, and all feeding occurred in the same area (50 m diameter). 'Amakihi are territorial during the nesting season (van Riper 1987, Lindsey et al. 1998), which suggests that only one male would occupy this small area. We know nothing about the reproductive effort of this 'Amakihi prior to or during its interactions with the Palila fledgling.

We observed the presumed parents of the Palila fledgling, both of which were wild-translocated birds, attempt at least four nests during 2006. Palila typically raise <1 fledgling per year and there are no records of more than three nests per female in 1 year (Banko

et al. 2002). Thus, the parents might have been unable to provide sufficient food to sustain three fledglings and themselves. Parental neglect could have encouraged the fledgling to actively pursue interspecific feeding opportunities (e.g., Verhulst and Hut 1996). We did not see the fledgling beg for food or otherwise interact with its parents or other nearby (<50 m) Palila, although the putative male parent fed the fledgling's presumed nest-mate on at least five occasions.

We have not detected evidence of brood parasitism between bird species on Mauna Kea (USGS, unpubl. data) and it seems likely the Palila we observed was adopted by the 'Amakihi after it fledged. The Palila fledgling was slightly more than twice the weight of an average male 'Amakihi (13.4 g) (Lindsey et al. 1998) and provisioning such a large fledgling would have been energetically demanding. The fledgling's high level of furcular fat suggests the 'Amakihi was devoting a large portion of its time to provisioning the Palila. Miller (1998) estimated four provisionings/hr for Palila fledglings during the first post-fledging week while van Riper (1980) observed 0.9 provisionings/hr. The rate of interspecific feeding we observed (1.1/hr) was at the lower boundary for intraspecific feeding rates at this stage of fledgling development.

The rarity of interspecific feeding suggests the behavior of the 'Amakihi was misdirected, either because of the super-normal stimulus provided by the Palila fledgling's size and begging behavior or by the loss of its own nest or offspring (Shy 1982). It seems unlikely the 'Amakihi benefited from its behavior, unless it gained needed experience in provisioning a fledgling.

ACKNOWLEDGMENTS

This research was made possible in part thanks to support from the Federal Highway Administration; the U.S. Army Garrison, Hawai'i; and U.S. Geological Survey wildlife research programs. We thank the Hawai'i Division of Forestry and Wildlife, and the U.S. Fish and Wildlife Service for access to study sites, and other assistance. We are grateful for administrative support from Hawai'i Cooperative Studies Unit (University of Hawai'i at Hilo) and Pacific Island Ecosystems Research Center. We also thank four anonymous reviewers for their helpful suggestions. We are especially grateful to the research interns who helped us in the field: M. R. Fredricks, M. A. Cacciapaglia, E. M. Olimpi, and B. S. O'Hare. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Banko, P. C., L. Johnson, G. K. Lindsey, S. G. Fancy, T. K. Pratt, J. D. Jacobi, and W. E. Banko. 2002. Palila (*Loxioides bailleui*). The birds of North America. Number 679.

Dróżdż, R., M. Hromada, and P. Tryjanowski. 2004. Interspecific feeding of a Great Grey Shrike (*Lanius excubitor*) fledgling by adult Yellowhammers (*Emberiza citrinella*). Biological Letters 41:185–187.

Johnson, L., R. J. Camp, K. W. Brinck, and P. C. Banko. 2006. Long-term population monitoring: lessons learned from an endangered passerine in Hawai'i. Wildlife Society Bulletin 34:1055–1063.

Lindsey, G. D., E. A. VanderWerf, H. Baker, and P. E. Baker. 1998. Hawai'i (*Hemignathus virens*), Kaua'i (*Hemignathus kauaiensis*), O'ahu (*Hemignathus chloris*), and Greater 'Amakihi (*Hemignathus sagittirostoris*). The birds of North America. Number 360.

Lozano, G. A. and R. E. Lemon. 1998. Adoption of Yellow Warbler nestlings by Song Sparrows. Wilson Bulletin 110:131–133.

McNair, D. B. and B. Duyck. 1991. Interspecific feeding among some oscines. Chat 55:9–11.

Miller, L. J. 1998. Behavioral ecology of juvenile Palila (*Loxioides bailleui*): foraging development, social dynamics, and helping behavior. Thesis, University of Maryland, College Park, USA.

Scott, J. M., S. Mountainspring, F. L. Ramsey, and C. B. Kepler. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Studies in Avian Biology 9:1–431.

Shy, M. M. 1982. Interspecific feeding among birds: a review. Journal of Field Ornithology 53:370–393.

van Riper III, C. 1980. Observations on the breeding of the Palila *Psittirostra bailleui* of Hawaii. Ibis 122:462–475.

van Riper III, C. 1987. Breeding ecology of the Hawai'i Common 'Amakihi. Condor 89:85–102.

Verhulst, S. and R. A. Hut. 1996. Post-fledging care, multiple breeding and the costs of reproduction in the Great Tit. Animal Behaviour 51:957–966.

Yoerg, S. I. and J. O'Halloran. 1991. Dipper nestlings fed by a Gray Wagtail. Auk 108:427–440.

The Wilson Journal of Ornithology 120(2):419–422, 2008

Adoption: Adaptation or Reproductive Error in Eastern Bluebirds?

Daniel P. Wetzel[1,2,3] and C. Ray Chandler[1]

ABSTRACT.—We describe an adoption event by a female Eastern Bluebird (*Sialia sialis*) and suggest a mechanism by which adoption could be adaptive. The foster female adopted three young and we were able to quantify two measures of parental care (nestling provisioning and nest defense). The foster female successfully reproduced with the father of the young in the same location later in the breeding season. The adopting female may be increasing her fitness by gaining future reproduction with a fertile mate at a productive nest box through parental care for young that are not related. *Received 12 March 2007. Accepted 6 October 2007.*

Adoption is the parental care of presumed non-linear offspring (PNLO) by an individual that is replacing the original parent and caregiver (Plissner and Gowaty 1988). The adaptive significance of adoption in birds is not well understood because it is thought to occur infrequently within populations, although 150 species of birds have documented cases of adoption (Avital et al. 1998). It is commonly assumed there is no direct benefit to an individual adopting another's young. Thus, adoption is usually referred to as "reproductive error". Reproductive error may be maladaptive as it occurs when an individual has strong environmental and behavioral cues to care for young, but their efforts are displaced to unrelated young (Rohwer 1986). It is assumed the adopting individual is not discriminating between its own and unrelated young. Avital et al. (1998) suggested that, although adoption seems to occur infrequently, there may be sufficient benefit for this trait to remain in a population. Individuals may adopt PNLO to gain access to mates or nest-sites, or to display their parental care to potential new mates (Gori et al. 1996). A new parent that can demonstrate its parental care may have an increased chance of re-nesting with a new mate (Rohwer 1986).

Mate replacement and adoption by the Eastern Bluebird (*Sialia sialis*) have been documented after male disappearance or experimental removal of males (Hamilton 1943, Kreig 1971, Pinkowski 1978, Gowaty 1983a). However, adoption by female Eastern Bluebirds is rare and the extent of parental care by adopting females is unknown (Gowaty 1983b, Rohwer 1986). This species is an obligate secondary cavity nester that breeds from late March through early August in the southeastern United States (Gowaty and Plissner 1998). Bluebirds are monogamous with bi-parental care of nestlings. Females typically lay 4–5 eggs in each clutch and lay up to three clutches per breeding season (Gowaty and Plissner 1998).

OBSERVATIONS

We describe a case of adoption by a female Eastern Bluebird in southeastern Georgia on a study area with several color-banded bluebirds and multiple nesting pairs in summer 2005. The study area was established in 2005 on 44.5 ha of open fields and contained 18 nest boxes. Nest box #4, with female F4 and male M4, hatched three young on 19 April and nest box #1 with female F1 and male M1, hatched two young on 23 April. The last known observation of female F4 at nest box #4 was on 17 April and the last known observation of male M1 from nest box #1 was on 24 April.

On 28 April, nest box #1, ~250 m from nest box #4, contained two dead nestlings, and two cold eggs, with no sign of either parent (F1 or M1). The deceased nestlings of female F1 would have been 6 days of age at that time, and the nestlings of male M4 at nest box #4 were 10 days of age. On that same day, provisioning and nest defense observations were performed at nest box #4. We quantified pro-

[1] Department of Biology, Georgia Southern University, Box 8042, Statesboro, GA 30460, USA.

[2] Current address: Department of Biology, 101 T. H. Morgan Building, University of Kentucky, Lexington, KY 40506, USA.

[3] Corresponding author; e-mail: dan.wetzel@uky.edu

visioning rates by observing the nest with a 20x spotting scope for 1 hr from a blind at ~30 m distance. Female F1 from nest box #1 was observed at nest box #4 with the original nest box #4 male, M4, provisioning the adopted nestlings at a rate of 1.67 times/chick/hr, while the original male M4 provisioned the nestlings 6.67 times/chick/hr. Mean (± SE) nestling provisioning rates for females and males on the study site were 1.91 (± 0.21) and 1.86 (± 0.24) provisions/chick/hr, respectively.

We quantified the defense responses of the new pair by placing a rubber eastern rat snake (*Elaphe alleghaniensis*) 0.5 m from the base of the nest box under a camouflaged cloth. The cloth was attached to a string operated from a blind ~20 m distance from the nest box. At a random time, after placing the snake under the camouflaged cloth and the parents had returned to normal activities, the string was pulled and the snake was revealed. Behaviors of both male and female bluebirds were observed for 14 min. The foster female, F1, performed investigative and nest defense behaviors at nest box #4 by landing on the top of the nest box three times to inspect and potentially deter the potential nest predator. During the same time, male M4 performed many defensive behaviors including chattering at the snake, wing flashing, and landing on top of the nest box to inspect and possibly deter the potential predator.

The three nestlings fledged from nest box #4 on 6 May. The new pair (female F1 and male M4) re-nested and initiated egg-laying in nest box #4 on 12 May; the pair fledged three young on 14 June. In the final nesting attempt at nest box #4, initiated on 27 June, three nestlings survived until 13 days of age, at which time they died with no signs of trauma or depredation. Foster female F1 returned to the study site in summer 2006 and nested successfully with another male on a territory adjacent to nest box #4. Male M4 was not observed at the study site in 2006.

DISCUSSION

We can identify three possible reasons for this adoption event by the female bluebird. First, the adopted nestlings may have been related to the foster female in some way. In this case, the female, with her own young dead, would increase her inclusive fitness by adopting related nestlings. This act is favored by selection, as the shared genetic material from the foster female would still be passed on in the related young. This is an unlikely scenario because, although breeding individuals do show some site fidelity from one season to the next (39–56% of breeding adults return to their previous year's nesting site), nestling dispersal from natal sites is much greater with only 11.9% of females and 14.6% of males returning to the natal study site (Gowaty and Plissner 1998). This suggests there is only a small chance the foster female was related to the original breeding pair (F4 and M4) or the nestlings she adopted. Inclusive fitness does not seem to be the reason for this adoption event.

Conspecific brood parasitism occurs in Eastern Bluebirds where females lay eggs in nests of other bluebird pairs but provide no parental care to the young (Gowaty and Plissner 1998). It is possible that female F1 parasitized the other breeding pair while female F4 was in the egg-laying cycle (Eastern Bluebirds usually lay 1 egg/day). By adopting the young at nest box #4, the foster female would be providing parental care to at least one of its own nestlings. Although possible, it seems unlikely that conspecific brood parasitism is the reason for the adoption event. The egg-laying cycle of female F1 had no overlap with female F4 (female F4 began incubating 2 days before female F1 began egg-laying), conspecific brood parasitism occurs infrequently in this species (1–2% of nestlings produced), and it has been suggested that females most likely to adopt the strategy of brood parasitism are females without their own nest boxes (Meek et al. 1994, Gowaty and Plissner 1998).

The second reason for adoption, reproductive error, is a likely scenario as most of the few cases of adoption in bluebirds occur when an individual has lost young of a similar age to the PNLO (Plissner and Gowaty 1988). Female F1 lost her nestlings, which would have been 6 days of age at the time of adoption, after the presumed desertion by her mate. The lone female joined with the lone male at nest box #4 and adopted the three 10-day-old nestlings. This female was possibly responding to physiological and behavioral cues evoked by her own young, which as a byproduct induced

the adoption of PNLO. This can be concluded because the foster female had young at approximately the same age as the adopted nestlings, there were other available, unused boxes in which to nest, and there was potential for 'floater' males in the area. Anecdotal evidence of Eastern Bluebird females that replace original breeding females suggests that replacement females will only adopt young when they are between 7 and 14 days of age (Plissner and Gowaty 1988, Gowaty and Plissner 1998). Nestlings that are <7 days of age tend to be left to perish or are killed and ultimately removed from the nest so the new pair can re-nest; nestlings that are >14 days of age are treated indifferently (Gowaty and Plissner 1998). The replacement female adopted PNLO that were 10 days of age, suggesting she could have misdirected parental behavior toward another's offspring. The foster female did not feed or defend the nestlings to the extent of the original male, but did feed an appropriate amount (not less than the mean female provisioning rate) for the number of nestlings. The male was feeding at a high rate, potentially the result of the perceived loss of the original mate.

The other likely cause of this adoption is the lone female was demonstrating her parental abilities to a new mate, and thereby gaining access to the male and a nest box. For adoption to be beneficial, the cost of the parental care to the female must be less than the benefit derived from the male genes and the quality of the breeding site. This is an adaptive cause for adoption, as the female would presumably be ensuring future reproduction with a fertile mate at a productive nest box by helping to care for PNLO. In areas where pairs have multiple broods, adoption may be a strategy that is favored early in the breeding season by individuals searching for a new mate (Rohwer 1986, Gori et al. 1996). Within-season mate replacement may be common in Eastern Bluebirds as only 35–60% of unsuccessful pairs and 70–85% of successful pairs will re-nest together in the same season (Pinkowski 1977). Bluebirds are socially monogamous in the breeding season suggesting that a lone bird may not have an available mate or a place to nest (Gowaty and Plissner 1998). There were several unused and available nest boxes in close proximity, but nest sites are historically limiting and this behavior may be a strategy to gain access to a potentially limited resource (Siefferman and Hill 2005b). Territory quality can vary widely and nest box #4 may have been on a particularly good territory. The foster female may have fed and defended the PNLO early in the breeding season to demonstrate her abilities as a parent and gain access to a mate, nest box, and/or territory. There is evidence that male mate choice may occur in Eastern Bluebirds (Siefferman and Hill 2005a). This is a potential cause for the adoption, as the new male and female pair successfully re-nested, produced six eggs, and fledged three young.

Many would assume that adoption is maladaptive, as it may simply be an act of displaced parental care. However, infanticide, which has been observed in many bird species including Eastern Bluebirds, is clearly not displaced parental care and is likely an adaptive behavior. Rohwer (1986) argues that although mate replacement may occur infrequently, it must have occurred often to select for infanticide, which suggests that mate replacement has been sufficiently frequent to eliminate adoption if it was maladaptive. Alternatively there may be strong selective pressure on parental care under normal contexts so selection against it in rare circumstances (like adoption) is relatively weak (Plissner and Gowaty 1988).

The described event is anecdotal and we illustrate the possible and reasonable interpretations of this adoption. We further suggest a mechanism for adoption to be adaptive in Eastern Bluebirds. It may be difficult to identify directly if and how adoption is adaptive; however, it is possible that studies examining this behavior could focus on the apparent quality of nest boxes, territory, and mates involved.

ACKNOWLEDGMENTS

We thank J. R. Brzyski, L. M. Siefferman, D. F. Westneat, and two anonymous reviewers for providing helpful comments and suggestions on the manuscript. We also thank Howard Lumber Company for donating lumber to construct nest boxes.

LITERATURE CITED

Avital, E., E. Jablonka, and M. Lachmann. 1998. Adopting adoption. Animal Behaviour 55:1451–1459.

Gori, D. F., R. Sievert, and J. Caselle. 1996. Ac-

cepting unrelated broods helps replacement male Yellow-headed Blackbirds attract mates. Behavioral Ecology 7:49–54.

GOWATY, P. A. 1983a. Male parental care and apparent monogamy among Eastern Bluebirds (*Sialia sialis*). American Naturalist 121:149–157.

GOWATY, P. A. 1983b. Overlap of two broods of Eastern Bluebirds in the same nest and brood reduction. Wilson Bulletin 95:148–150.

GOWATY, P. A. AND J. H. PLISSNER. 1998. Eastern Bluebird (*Sialia sialis*). The birds of North America. Number 381.

HAMILTON JR., W. J. 1943. Nesting of the Eastern Bluebird. Auk 60:91–94.

KREIG, D. C. 1971. The behavioral patterns of the Eastern Bluebird. New York State Museum and Science Service Bulletin Number 415.

MEEK, S. B., R. J. ROBERTSON, AND P. T. BOAG. 1994. Extrapair paternity and intraspecific brood parasitism in Eastern Bluebirds revealed by DNA fingerprinting. Auk 111:739–744.

PINKOWSKI, B. C. 1977. Breeding adaptations of the Eastern Bluebird. Condor 79:289–302.

PINKOWSKI, B. C. 1978. Two successive male Eastern Bluebirds tending the same nest. Auk 95:606–608.

PLISSNER, J. H. AND P. A. GOWATY. 1988. Evidence of reproductive error in adoption of nestling Eastern Bluebirds (*Sialia sialis*). Auk 105:575–578.

ROHWER, S. 1986. Selection for adoption versus infanticide by replacement "mates" in birds. Current Ornithology 3:353–395.

SIEFFERMAN, L. AND G. E. HILL. 2005a. Evidence for sexual selection on structural plumage coloration in female Eastern Bluebirds (*Sialia sialis*). Evolution 59:1819–1828.

SIEFFERMAN, L. AND G. E. HILL. 2005b. UV-blue structural coloration and competition for nestboxes in male Eastern Bluebirds. Animal Behaviour 69:67–72.

The Wilson Journal of Ornithology 120(2):422–424, 2008

An Intraspecific Killing in Adult Pacific Reef Egrets (*Egretta sacra*)

Christa Beckmann[1,2]

ABSTRACT.—Intraspecific killing without cannibalism is rare in birds. I report an observation of an adult Pacific Reef Egret (*Egretta sacra*) killing an adult conspecific at One Tree Island, Great Barrier Reef, Australia. The motivation and context for the killing were not apparent. To the best of my knowledge, this is the first report of intraspecific killing in Pacific Reef Egrets. *Received 18 June 2007. Accepted 12 September 2007.*

Intraspecific killing in birds occurs occasionally and may or may not represent cannibalism. Whereas cannibalism of eggs and chicks is not uncommon in birds (Stanback and Koenig 1992), killing without cannibalism is rare. Killing without cannibalism may result from territorial disputes (Flux and Flux 1992), siblicide (Fujioka 1985), and infanticide (Parkes 2005). In the rare situation of an adult killing a conspecific adult, there are indications that victims may be in poor physical condition (Franklin's Gull [*Larus pipixcan*], Brose 2006; Ruddy Turnstone [*Arenaria interpres*], Crossland 1995). These instances are not well described and why it occurs is uncertain. Most reports are based on anecdotal evidence (House Wren [*Troglodytes aedon*], Belles-Isles and Picman 1987; Smooth-billed Ani [*Crotophaga ani*], Loflin 1982; Great Gray Owl [*Strix nebulosa*], Fisher 1975; Red-tailed Hawk [*Buteo jamaicensis*], Clevenger and Roest 1974; Tree Swallow [*Tachycineta bicolor*], Lombardo 1986; Lesser Snow Goose [*Chen caerulescens caerulescens*], Hick and Cooke 1988) rather than direct observations (Northwestern Crows [*Corvus caurinus*], Andersen 2004; House Sparrows [*Passer domesticus*], Grubbs 1977). This note describes the first observation of an adult Pacific Reef Egret (*Egretta sacra*) killing an adult conspecific and suggests possible reasons why killing may occur.

OBSERVATIONS

I observed a dark morph Pacific Reef Egret attacking a white morph egret at One Tree Island, Great Barrier Reef, Australia (23° 27′ N, 152° 3′ E) on 9 February 2007 at 0746 hrs. The event occurred on the island between two

[1] Department of Environmental Sciences, University of Technology, Sydney, P. O. Box 123, Broadway NSW 2007, Australia.

[2] Current address: School of Biological Sciences, University of Sydney, NSW 2006, Sydney, Australia; e-mail: cbec6408@mail.usyd.edu.au

of the field station buildings on and beside a foot path. The area consists of coral rubble substrate and is sparsely vegetated with Pisonia (*Pisonia grandis*) trees, ~1.5 m tall. The event was observed from both inside one of buildings from the window and when the birds were out of view from the window, I continued observations from outside, standing close to the building. Observations were made either with or without 10 × 42 binoculars at distances of ~15 m (from window) to 30 m (outside) from the birds.

I observed the dark morph egret stabbing the white morph bird on and around the head with its bill while the white morph was sitting on its legs with its head down and covered in blood. A second dark egret was perched on the railing of a nearby building, watching. The aggressor took two steps back and then ran at the white egret, stabbing it in the head. At 0748 hrs the dark morph left and returned 2 min later. It stood with one foot on the back of the white egret, essentially pinning it to the ground while stabbing it repeatedly. It then stood on the back of the white egret with both feet while attacking the white egret around the head. Six minutes later the white egret tried to escape, running with head down and wings outstretched. The dark egret chased closely after it, pulling on its wing feathers. The white egret moved ~10 m away and the dark egret then left at 0755 hrs. At 0800 hrs the two dark morph egrets returned. One bird attacked the white egret stabbing it twice in the head and both left again, 3 min later. At 0833 hrs, one dark egret returned and perched on the balcony of a nearby building. At 0836 hrs the dark egret flew to the ground and stabbed the white egret four times in the head. A second dark egret arrived 1 min later and stood nearby, observing. The white egret walked ~4 m away and both dark egrets left at 0838 hrs. A dark egret was seen in the area at 0955 hrs, but was not observed attacking the white egret. In total, 52 min elapsed between when observations began (at which point the victim was already covered in blood), and when the last attack by the dark morph egret was observed. I checked the condition of the white egret at 1500 hrs. It was still alive, but was lying on the ground with eyes closed. It later died and I then examined the carcass. The bird was an adult and not in breeding condition. It was not in molt and had wounds on and about the head only, which was covered in blood. The bird appeared to have been in poor condition as the keel was totally exposed with no fat or muscle tissue. I assumed that only one dark morph egret was responsible for the attack(s).

DISCUSSION

This note documents an adult Pacific Reef Egret killing an adult conspecific and, to the best of my knowledge, is the first report of an adult Ardeidae species killing a conspecific adult. Cannibalism did not appear to be the motivation of this killing as the dark egret did not feed upon the white egret.

Disputes over resources, (particularly food, offspring, mates, and territory) seem likely underlying reasons for intraspecific killing (without cannibalism) among adult birds (Flux and Flux 1992). It is possible the killing occurred over a dispute, perhaps over territory. The white egret did not show signs of being in breeding condition (i.e., no brood patch, cloacal protuberance, or breeding plumage) and was in poor body condition, and likely starving. The dark egret was not in breeding plumage, nor was the dark morph bird which observed only. Therefore, it is not likely the dark egret could have been defending breeding territory, eggs or chicks. Individuals are known to defend foraging territory; however, aggressive displays between birds are simple and brief (Marchant and Higgins 1990). Submissive birds either leave the area or adopt the withdrawn crouch display (sitting on their legs with head tucked in) and the aggressor then halts its attack (Marchant and Higgins 1990). The white morph, being in poor condition, may have been unable to leave the territory of the dark egret before being severely damaged. The dark egret may have continued the attack until the white egret was outside its territory. That the second dark egret was not attacked by the aggressor places doubt on the theory that it was defending a foraging territory. Little is known about the territorial behavior of this species (Marchant and Higgins 1990) and, as my observations began when the attack was underway, any conclusions on this issue are speculative.

In two other reported observations of intraspecific killing, the victim was in poor body

condition (Crossland 1995, Brose 2006). In both cases, there was more than one aggressor as well as other individuals watching. It is possible the motive for this attack was somehow related to the poor condition of the victim.

Future research into when and why adult intraspecific killing occurs should involve more observations of intra-specific aggression, and could involve presentation of taxidermy models of conspecifics and documentation of aggressive behavior.

ACKNOWLEDGMENTS

I thank P. A. Biro and two anonymous reviewers for helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

Andersen, E. M. 2004. Intraspecific predation among Northwestern Crows. Wilson Bulletin 116:180–181.

Belles-Isles, J. C. and J. Picman. 1987. Suspected adult intraspecific killing by House Wrens. Wilson Bulletin 99:498.

Brose, C. 2006. Franklin's Gulls kill wounded individual. Blue Jay 64:215.

Clevenger, C. T. and A. I. Roest. 1974. Cannibalism in Red-tailed Hawk. Auk 91:639.

Crossland, A. C. 1995. A probable case of intraspecific killing in turnstones (*Arenaria interpres*). Notonis 42:281–282.

Fisher, B. M. 1975. Possible intraspecific killing by a Great Gray Owl. Canadian Field-Naturalist 89:71–72.

Flux, J. E. C. and M. M. Flux. 1992. Nature red in claw: how and why starlings kill each other. Notornis 39:293–300.

Fujioka, M. 1985. Sibling competition and siblicide in asynchronously-hatching broods of the Cattle Egret *Bubulcus ibis*. Animal Behaviour 33:1228–1242.

Grubbs, V. L. 1977. An intraspecific mortal attack. Wilson Bulletin 89:477.

Hick, D. S. and F. Cooke. 1988. A possible case of intraspecific killing in the Lesser Snow Goose. Wilson Bulletin 100:665–666.

Loflin, R. 1982. Ani male apparently killed by other Anis while attempting to parasitize nest. Auk 99: 787–788.

Lombardo, M. P. 1986. A possible case of adult intraspecific killing in the Tree Swallow. Condor 88: 112.

Marchant, S. and P. J. Higgins (Editors). 1990. Eastern Reef Egret. Pages 1002–1009 *in* Handbook of Australian, New Zealand and Antarctic birds. Volume 1, Part B. Ratites to ducks, Oxford University Press, Melbourne, Australia.

Parkes, M. L. 2005. Inter-nest infanticide in ardeids. Waterbirds 28:256–257.

Stanback, M. T. and W. D. Koenig. 1992. Cannibalism in birds. Pages 277–298 *in* Cannibalism: ecology and evolution among diverse taxa (M. A. Elgar and B. J. Crespi, Editors). Oxford University Press, New York, USA.

The Wilson Journal of Ornithology 120(2):425–431, 2008

Ornithological Literature

Compiled by Mary Gustafson

BIRDS OF THE ALEUTIAN ISLANDS, ALASKA. By Daniel D. Gibson and G. Vernon Byrd. Nuttall Ornithological Club and American Ornithologists' Union, Series in Ornithology Number 1. 2007. ISBN: 978-0-943610-73-3. 351 pages, 18 color plates, 2 figures. $40.00 (cloth).—The Aleutian Islands, Alaska, covers some 1,800 km of longitude, bridging the gap between Nearctic and Palearctic faunas. Also spanning some 475 km of latitude, their location between 50–55° N—at the boundary between the North Pacific Ocean and Bering Sea—places them in the middle of an exceptionally dynamic zone of cyclogenesis, an area dominated for much of the year by "the Aleutian Low" resulting in a cool, wet, maritime climate frequented by major storms. At least two of these islands have coined themselves as the "The Birthplace of the Winds." These winds are largely the cause of an archipelago-wide vegetation type dominated by grasses, herbs, and dwarf shrubs; only in the most protected pockets are taller shrubs to be found.

These remote islands are home to a fascinating blend of western and eastern birdlife, as well as a unique, localized "Beringian," avifauna. They support staggering nesting populations of millions of alcids and other seabirds. The isolated location of much of the chain results in its not being on the principal migration routes of many species with the exception of some waterfowl and shorebirds. The Aleutians are a fascinating area for study of vagrancy in both Asian and North American species, including many landbirds. A large number of birds may be carried east from Japan and the Russian Far East to these islands by major storm systems that track east and northeast in both spring and fall from the Asian coast, across the Aleutian chain, and onward into the southern Bering Sea or Gulf of Alaska.

Two authorities have studied the avifauna of the Aleutian Islands in greater depth than anyone else: Daniel D. Gibson and G. Vernon Byrd—Gibson primarily through his many years as collections manager at the University of Alaska Museum, and Byrd through his position as supervisory wildlife biologist for the Alaska Maritime National Wildlife Refuge. For some 35 years they visited nearly every one of the Aleutian Islands, combining this intimate knowledge with a thorough review of the published literature and an exhaustive museum search for archived specimens and photographs. The result is an exceptionally thorough inventory of the avifauna of the Aleutian region, including all the islands of the chain as well as data from waters offshore.

Following short introductory sections describing the physiography, climate, habitats, and history of ornithological study in the region, the lion's share of the book is taken up with detailed individual species accounts which cover the 271 species (plus 28 additional subspecies) recorded through 2005 and substantiated by specimens or photographs. (Those species documented only by written details are included in an appendix.) Each account is organized by dividing the Aleutians in to three sub-groups: the Eastern Aleutians (Fox Islands and Islands of Four Mountains), Central Aleutians (Andreanof and Rat islands), and Western Aleutians (Buldir and Near islands). Within each of these groups, species' occurrence is presented by season, and the information includes data on seasonal abundance, early and late dates, maximum counts, habitat, and, when relevant, estimated nesting population sizes. In addition, there are color photographs grouped in the center of the book which depict a few birds and the different Aleutian habitats. In the back of the book, there is brief analysis of the seasonal movement of birds within the island chain, and more thorough looks and helpful tabular comparisons of habitat use, egg-laying dates, and early arrival and late departure dates. Also included is a gazetteer. There is discussion of the substantial changes to habitats and bird populations brought on by hunting, military activities, and the widespread introduction of mammalian predators including rats and foxes, as well mention of the recent projects to

eradicate some of these harmful species and the results to date.

This is an exhaustive treatise. The depth of the ornithological record presented is exceptional. Details concerning many of the unique and fascinating taxonomic problems and uncertainties encountered in this region at both the species and subspecies level are covered. This reviewer could not find anything of substance included within the book's covers with which to find fault. However, the chosen font and format of the accounts make them somewhat hard to read and it is difficult to quickly scan an account to find the specific section desired. Hopefully, future volumes in this new *Series in Ornithology* will have a more user-friendly print and layout. In regards to the book's content, I wish that the authors had included *more.* Yes, it is easy to stand on the sidelines and want writers to include yet more information in many of their books. In the case of *Birds of the Aleutian Islands, Alaska* it might seem particularly undeserving to ask for more given the amazing depth and breadth of information presented. Yet, as the volume describes itself, it is indeed an "inventory."

There is little discussion on theories of occurrence such as vagrancy to the Aleutians and the possible effects of major meteorological events. Nor do more than a handful of the species accounts place records into a larger perspective comparing occurrences to those elsewhere in Alaska, East Asia, or similar latitude. Each account *does* include a brief, single-sentence description of the species' overall range and, for rare visitors from the Alaska mainland, mention is made of how close to the Aleutians they nest. An account of the questionable occurrence of Willow Ptarmigan (*Lagopus lagopus*) anywhere but on the eastern-most island (Unimak) includes a fine discussion of other records of Willow and Rock (*L. muta*) ptarmigan making major sea/ice crossings in both eastern Russia and western Alaska. But, such discussions are rare. Many accounts of other migrant and vagrant species would have profited by just brief mention of how these Aleutian records fit into the broader picture of avian occurrence in at least the Bering Sea and northernmost Pacific Ocean regions. For example, the single, exceptional Aleutian record for Sooty Tern (*Sterna fuscata*) involved remains of an adult salvaged on Attu Island in September 1997, but the account does not include mention of the previous passage of extra-tropical typhoons (probably the most likely mechanism of transport) or if there exist *any* other records of this species northeast of Japan. The account of the single Aleutian record of Purple Martin (*Progne subis*) would have benefited from mention of its status in Alaska. The single record of Wood Warbler (*Phylloscopus sibilatrix*) from October 1978, which established the first North American record of this Western Palearctic species, would have been placed in better perspective with mention of a subsequent (October 2004) record from the nearby Pribilof Islands and of there being multiple autumn records from Japan. These comments would help the reader in gaining a much better perspective on such occurrences.

Overall, this is a truly monumental, scholarly work. Its thoroughness in treating the fascinating avifauna of the Aleutian Islands will be invaluable to researchers and to students of bird distribution throughout North America and the Pacific Rim.—PAUL LEHMAN, 11192 Portobelo Drive, San Diego, CA 92124, USA; e-mail: lehman.paul@verizon.net

ATLAS OF BIRD DISTRIBUTION IN NEW ZEALAND 1999–2004. By C. J. R. Robertson, P. Hyvonen, M. J. Fraser, and C. R. Pickard. The Ornithological Society of New Zealand, Nelson, New Zealand. 2007. 533 pages, 2,100+ maps. ISBN: 0958248656. $125.00 (cloth).—As a member of the Ornithological Society of New Zealand, I received my copy of this impressive tome gratis; this is just as well, as it is a large (30.5 × 21.5 cm), heavy (2.5 kg) book with a substantial price tag. When I describe this book as impressive, the word is well-chosen. This is a quality product with clearly-printed maps, interesting commentary on each species, useful interpretation of the data, and extensive use of appendices which present data associated with the atlas effort.

Atlas efforts began in New Zealand in 1969 when field observers were encouraged to provide lists of species from 3,675 squares covering the country (North, South, and Stewart islands), each square containing 9,144 m^2 (10,000 yds^2). This effort was summarized in

a provisional atlas published in 1978 which included data collected through 1976 (Bull et al. 1978). This small book was followed by a more substantial version published in 1985 (Bull et al. 1985) which covered the years 1969–1979 and incorporated the data included in the 1978 provisional atlas. The 1985 atlas contained 19,049 species lists from the 3,675 squares. The book, subject of this review, summarizes data contained in 31,817 species lists from 3,192 squares, now 10 km^2 each, throughout North, South, and Stewart islands with the addition of the Chatham Islands. It is described in the Introduction (page 8) thus: "This bird distribution atlas demonstrates dramatic and rapid change in bird distribution in all parts of the country. These data provide the challenge of questions that need urgent answers . . . "

A wide range of information is presented in the 533 pages in addition to the expected distribution maps. The Introduction (8 pages) provides a good overview of the atlas process, in particular collection of field data and the technical aspects of the data processing systems used. An important section of the Introduction discusses various problems inherent in the effort, such as nomenclature, treatment of rarities, and treatment of breeding records. These issues are clearly obvious targets for critics, and I believe these potential short-falls are countered, or at least explained, well in this section. The authors are cognizant throughout that there are well-known problems with distributional atlases for which data are mostly collected by amateurs and especially those, like this one, that are based on simple species lists. The basic goal of any atlas should be the simple presentation of distribution data. Users of the data must temper their efforts by acknowledgment of the inherent short-falls. The Introduction concludes with an interesting series of potential uses for the atlas data. Prominent among these are the "significant observed changes in gross distribution . . . for 57% of the birds" included in this atlas and its 1985 predecessor (detailed in Appendix K). This result is the key reason that an atlas is undertaken; the authors note these data provide an important baseline for further study. Prominent in New Zealand are its fascinating endemic species; these are of primary concern in conservation, efforts conducted in often spectacular and well-publicized fashion in New Zealand (Black Robin [*Petroica traversi*], Kakapo [*Strigops habroptila*], and Kiwi [*Apteryx* spp.]). Among endemics, increases in gross distribution were found for 15 species, with 25 reduced, and 26 without change. Native and introduced taxa generally had increases, some rapid, over their distributions in the 1985 atlas. It is important to remember that the data presented in the atlas do not allow conclusions regarding numbers of individuals present.

There follows a relatively short (7 pages) discussion on aspects of analysis of the data; weaknesses are discussed, mostly inherent biases resulting from variations between observers in the process of data collection and the details provided, especially related to habitat and breeding behavior descriptions. This section provides useful information and caveats for future users of the data.

The bulk of the atlas is the almost 300 pages of species distribution maps, followed by some 40 pages of maps depicting habitats reported by observers. A nice touch is inclusion with the atlas of a transparent plastic bookmark-sized overlay tool inscribed with the three differing-scale matrixes of grid squares used in the atlas. This tool is useful in helping the reader differentiate and identify squares in a locality of interest.

Each species has a full page distribution map for North Island and South Island (Stewart Island is included with South Island); several species occur on only one of the major islands. The maps also include distributions for the Chatham Islands, an addition since the 1985 publication. Each square where the species was found is marked with a red spot super-imposed on clearly-printed relief maps. An attempt to indicate relative abundance is made by using a range of four sizes of spots, the smallest indicating the species was found on $<10\%$ of the lists submitted for that square, and largest spot for over 60%. The introduction to the map section (page 19) reports potential inaccuracies in this method, noting its non-use for taxa for which there are fewer than 50 reports in all; interpretation of these variable-sized spots requires care, as the authors indicate: "This division of results produces a probable over-emphasis for single-sheet reports for a square . . . " At best, this

method provides only a rough indication of relative abundance.

Each map page presents additional information of five types with varying usefulness. Most significant is a brief (rarely more than 4 lines) commentary at the bottom of each page which discusses changes from the 1985 atlas, suggests reasons for these changes where known, includes taxonomic notes, and provides a useful set of literature citations for the species. I found these text entries to be the most valuable part of the overall effort. Taken together with the maps, these entries provide the reader with an excellent overview of the current status of each species. Not so useful are reproductions on each map page of the distribution map for that species in the 1985 atlas. Presumably this was done to allow a quick comparison with the 1985 distribution but, unfortunately, these reproductions are small and I found it difficult to discern changes in distribution except for a few large-scale expansions or contractions; the information provided in the text comments is far more useful.

Leading off each map page are English, Latin, and Maori names for the species, its status, its 6-letter code (as compared to the 4-letter banding codes generally used in the United States), and the number and percentage of squares and list sheets where the species was observed. English and Latin names presented the authors with a problem, as the most recent Checklist of New Zealand birds (Turbott 1990) is clearly dated, both taxonomically and with respect to the recently-controversial issue of standardization of English names internationally. Although a new Checklist is imminent, the authors chose to follow Turbott (1990) with changes or updates noted in the text on each page. I found these latter notes useful and informative. The topic of English names is hotly-debated, but I lean to use of the name traditional in the country where the species is endemic as a first choice. Generally this is the name used on the map pages. As with many names used by indigenous peoples, Maori names vary regionally. The authors indicate they have used a list provided to them by the Maori Language Commission, but have included additional names that have been used in the past in ornithological works. The descriptors used to describe status are simply-defined: Endemic (breeds only in New Zealand territories), Native (breeds in New Zealand territories and elsewhere), Migrant ("a reasonable number" migrates to New Zealand territories but does not breed), Straggler (or Vagrant; "not a regular migrant", or few migrate to New Zealand territories, but do not breed), and Introduced ("introduced by *Homo sapiens*"). While these definitions could be tightened, I must say as a tour operator catering to bird-listers, that the definition of "Endemic" as a species that breeds only in New Zealand greatly simplifies the determination of which species are New Zealand endemics, notably seabirds that breed on a few islands in New Zealand but have large oceanic distributions (i.e., Black Petrel [*Procellaria parkinsoni*], Cook's Petrel [*Pterodroma cookii*]). It should be noted that most definitions of "Endemic" (such as: unrecorded away from the country in question) would not cover these two procellariids.

In addition, each map page has four small maps, one for each season, purporting to show differences in seasonal distribution, and another small map depicting breeding records. Migration among land birds in New Zealand is assumed to be minimal with the exception of possible altitudinal movements; these maps confirm this knowledge, but I had difficulty discerning whether there were differences or not. To test my ability to discern these, I checked the maps for Shining Bronze and Pacific Long-tailed cuckoos (*Chrysococcyx lucidus*, *Urodynamis taitensis*), both of which essentially depart New Zealand during the austral winter. These maps show significant seasonal differences, although it is important to note the seasons are defined as 3-month periods, a method that does not consider variations in breeding phenology and migration timing between species. Shorebirds which breed in New Zealand are strongly migratory in many cases, and these movements are shown well by the seasonal maps, as are presence and absence of seabirds that breed around New Zealand. I found the maps for migratory shorebirds visiting New Zealand less informative; for most there were few squares involved and those shown as occupied probably reflect the presence of suitable habitat (this information is useful, but is depicted in the habitat maps shown later in the atlas).

The remaining data presented on each map

page, again as small maps, show the squares in which breeding was reported. Perhaps the least useful of the information presented, the authors state (page 38): "For most taxa the availability of breeding records from the survey is very poor, or poorly distributed, and the maps record only what was reported." Atlases with which I am most familiar are those from Iowa and Nebraska; these are usually described as "breeding bird" atlases, and put far greater emphasis on a hierarchy of firmness of evidence indicating breeding. The New Zealand atlas does not purport to be a "breeding bird" atlas, but is entitled a "bird distribution" atlas.

I found the maps informative and easy to use. The maps are best for land birds, but are weak in depicting distribution of seabirds, other than those which breed on islands near the coast of the main islands. The data are too few to be meaningful for other seabird species. It seems likely the distributions shown for several of these reflect the availability of offshore boat trips rather than true distributions of the seabirds. Good examples are the distributions shown for Shy Albatross (*Thalassarche cauta steadi*, *T. c. salvini*), both of which contain excellent representations of the route followed by the Cook Strait ferries.

Following the distribution maps is a series of 40 pages of habitat maps. These show habitats reported by observers for surveyed squares and are subdivided to be useful indicators of habitat distribution. A notable example is the sub-division of "Native Forest" into Kauri, Podicarp, Tawa, Beech, Rata/Kamahi, Mixed Hardwoods, Manuka/Kanuka, and Shrubland. Maps I found somewhat novel, but informative, are sub-alpine scrub, scree/rock and herbfield, introduced pine, orchard, and market garden/crops. Coastal habitat is subdivided into several categories, including estuary/mudflat, lagoon, harbor, and rocky coast, but some are so widely-distributed and close to each other that it is difficult to obtain useful information from the maps. Finally, there are 7 maps using red dots of four sizes to indicate the number of taxa reported in squares in "grouped habitats". I found these maps useful; the grouped habitats are native forest, exotic plantation, farmland, residential, wetland, and coastal.

Most atlases are content to present distributional data in the form of maps with more or less textual commentary. This atlas, however, does not stop there. To complete the main body of the book are two interesting sections, Data Use Examples, and Biodiversity. Both provide interesting examples of use of the atlas data.

The 20-page Data Use Example section has a series of maps that show squares covered by the most active observers; observer #2211 covered almost the entire North Island! Also in this section are interesting "Comparative" maps; one shows squares with grouped alpine habitat using an orange dot, New Zealand Rockwren (*Xenicus gilviventris*) in pink, and squares with both in green. The green dot squares indicate the limited distribution of Rockwren as well as their apparent absence from large areas of alpine habitat. I couldn't find any pink dots; apparently there weren't any (Rockwrens shouldn't occur in non-alpine habitat), or perhaps the pink color was too similar to the orange to be easily discerned. There follow two articles reporting innovative uses of atlas data, which make for interesting reading as well.

The final 31 pages of the main body of the atlas (except for References) cover Biodiversity. This section uses data in the species map section and modifies them using smoothing software. These maps allow easier visualization of combinations of data such as occurrence by square and number of taxa per square. Thus, in areas where a number of squares are occupied by higher numbers of taxa, the color hue is darker; the hue lightens as these numbers decline. Most interesting among these maps are those showing distribution of endemic and introduced taxa, and a series showing distribution of endangered taxa ranging from most threatened to least threatened. The final map in this section (page 410) is a thought-provoking inversion of the smoothed map showing current distribution of extant endemic taxa; it is based on the premise that "the areas most affected by human influences were those with the richest and most biodiverse environments." This map suggests that before humans arrived, taxa were most numerous in the eastern South Island, particularly southward, where a wider range of habitats exist. Unfortunately, at least 50% of these pre-human taxa are now extinct.

The Reference section concludes the main body of the atlas; it is extensive and valuable. The only complaint I have is that it is subdivided (General References, Atlas References, Classified Summarized Notes, Taxon References); this often leads to extra time locating a citation.

The atlas presents 12 Appendices and an Index. Appendices A through E essentially summarize the data provided on field observer list cards, including monthly data and grouped habitat data. Appendix F is an interesting ranking by grouped habitat of species observed; thus New Zealand Pipit (*Anthus novaeseelandiae*) was the most-often observed species in alpine habitats, Grey Gerygone (*Gerygone igata*) in Native Forest, European Starling (*Sturnus vulgaris*) in Farmland, and Common Chaffinch (*Fringilla coelebs*) in Exotic Plantations. Appendices G and I were of interest from a bird listing viewpoint; Appendix G lists distribution records not shown on a map, being the rarest of the species reported. They range from oddities such as Emu (*Dromaius novaehollandiae*), through locally-distributed rarities like South Georgia Diving-petrel (*Pelecanoides georgicus*), and vagrants such as Ruff (*Philomachus* pugnax) and Common Greenshank (*Tringa nebularia*). Appendix I lists species unrecorded during the 1999–2004 atlas field surveys but, which were included in the 1985 atlas (e.g., Hoary-headed Grebe [*Poliocephalus poliocephalus*], South Island Bushwren [*Xenicus longipes longipes*], and two species of Wood-swallow [*Artamus*]) or are now known to breed in New Zealand but were not reported in 1999–2004, mostly island endemics outside the geographic scope of this atlas. Appendix H is a list of observers and the numbers of list sheets, squares, and taxa reported by each; I discovered here that observer #2211 is Tadeusz Wnorowski. Appendix J reproduces Instructions to Contributors as presented on field cards. Appendix K is an important summary of observed changes in distribution between this atlas and the 1985 version; this Appendix summarizes the results of the 1999–2004 atlas survey. The 137 species included provide much food for thought and grist for further investigation. The final Appendix, L, lists total number of lists returned, and top squares for lists returned, number of taxa, and taxa per square.

I recommend this book to anyone interested in the birds of New Zealand. Although it is large and expensive, bordering on being quite acceptable and impressive as a coffee-table exhibit, it has something for everyone, from the researcher to the dedicated bird-lister. It will no doubt be of most use as a spring-board for further study of the distributional changes revealed within, especially those hitherto unsuspected. Both positive and negative changes in distribution are significant; conservationists and land developers would do well to study this atlas with a view to consequences of their activities.—ROSS SILCOCK, P. O. Box 57, Tabor, IA 51653, USA; e-mail: silcock@rosssilcock.com

LITERATURE CITED

Bull, P. C., P. D. Gaze, and C. J. R. Robertson. 1978. Bird distribution in New Zealand, a Provisional Atlas. The Ornithological Society of New Zealand Inc., Wellington, New Zealand.

Bull, P. C., P. D. Gaze, and C. J. R. Robertson. 1985. The Atlas of bird distribution in New Zealand. The Ornithological Society of New Zealand Inc., Wellington, New Zealand.

Turbott, E. G. 1990. Checklist of the birds of New Zealand and the Ross Dependency, Antarctica. Random Century, Auckland, New Zealand.

RAPTORS OF EASTERN [WESTERN] NORTH AMERICA (2 volumes). By Brian K. Wheeler. Princeton University Press, Princeton, New Jersey, USA. 2003: 439 pages, 562 photographs, and 36 maps [2003: 544 pages, 630 photographs, and 54 maps]. ISBN 0-691-13476-5 [ISBN 0-691-13477-2]. Price per volume $29.95 (paper).—We have come a long way in identifying raptors in the field since the first modern field guide, Roger Tory Peterson's *A Field Guide to the Birds,* was published in 1934.

Peterson's guide illustrated 23 species of eastern birds of prey with 33 images on four plates and one line drawing. Wheeler's "eastern" volume of the currently reviewed two-volume work illustrates the same 23 species, plus three additional mainly western raptors, with 562 photographic images spread across 147 pages. Peterson's book devoted 16, 11.5 × 18.5-cm pages of text and illustrations to raptors. Wheeler's "eastern" volume devotes

439, 14.5 × 23.5-cm pages of text and illustrations to the group. The difference is readily apparent when one compares a single species. Wheeler's "eastern" volume spends 43 pages, 82 color photographs, and 5 maps on Red-tailed Hawk (*Buteo jamaicensis*). Peterson spent 25 lines of text and one black-and-white illustration on the same species. To say the two books are different is an understatement.

Wheeler's two volumes also differ significantly in approach from the highly acclaimed, 254-page *Hawks in Flight* by Pete Dunne, David Sibley, and Clay Sutton (1988), which, at the time, adopted a holistic, gestalt, or "gizz" attitude to identifying flying birds of prey. According to Wheeler "Identifying raptors is much like assembling a puzzle: you do it piece by piece." And piece by piece, subspecies by subspecies, and color morph by color morph, is, in fact, the approach that Brian Wheeler takes throughout this meticulously well-written, well-researched, and well-illustrated field guide and handbook. For those who have yet to see the work, Wheeler's two volumes most closely resemble Dick Forsman's similarly detailed, *The Raptors of Europe and the Middle East: A Handbook of Field Identification* (1999), albeit with considerably more text.

Wheeler begins his "eastern" volume with 34 pages of introductory material in seven chapters that cover anatomy, plumage, molt, age differences, perching, and flight behavior, together with some background on his photography. The section includes five glossaries detailing more than 250 terms, including, for example, four types of albinism and four types of flight-profile dihedrals. The glossaries are helpful, if not necessary, adjuncts to the detailed yet telegraphic species accounts that follow.

One of the greatest contributions of the work is its detailed, precise, and largely accurate range maps (36 in the "eastern" volume and 54 in the "western"). Although they are likely to fall out-of-date quickly as the ranges of several species fluctuate overall, and as the migratory behavior of many species changes the demarcation lines of summer and winter ranges, Wheeler's range maps will continue to serve as a useful historic record of the summer, winter, and year-round ranges of North American raptors for some time. A suggestion is in order here: a web site with 5-year updates of range maps would provide a useful addition to the work.

Wheeler's photographs, which are wonderful individually, and are spectacular when grouped together in species portfolios, are in some ways the heart and soul of the work. My only suggestion is that the location at which each photograph was taken be included in the legend, should the book be reprinted.

Wheeler's attempts to identify the full range of sub-species differences in field identification are both laudable and exhausting. The devil, as they say, is in the details, and, much to his credit, Wheeler spends considerable time dealing with this "hellaciously" complicated aspect of raptor field identification.

The true mark of any great field guide is that it serves as a useful reference for workers in the field: something that both the beginning and experienced hawk watcher will use again and again, not only to teach themselves, but also to teach others about important field marks and identification cues. Wheeler clearly succeeds in meeting this goal. Although the work is not the easy read of a Peterson (1934) or a Dunne, Sibley, and Sutton (1988) and, although it is not a work that one is likely to take into the field regularly, together the two volumes are essential reference for bird-of-prey field identification and distribution that should be in the possession of all raptor aficionados, professional and amateur. Even though the two volumes overlap extensively in both content and photographs, the range maps and parts of the text dealing with each species' areas of occurrence differ, and having both will be important to those interested in each species' North American range.

Finally, I must say that I cannot imagine anyone writing and successfully publishing more detailed descriptions of raptor field marks in a stand-alone field guide. What needs to occur next is for someone to boil down the complexity Wheeler has identified, so that those of us without encyclopedic memories can identify North America's birds of prey in the field . . . at least most of the time.—KEITH L. BILDSTEIN, Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, 410 Summer Valley Road, Orwigsburg, PA 17961, USA; e-mail: Bildstein@hawkmtn.org

THE WILSON JOURNAL OF ORNITHOLOGY

Editor CLAIT E. BRAUN
5572 North Ventana Vista Road
Tucson, AZ 85750-7204
E-mail: TWILSONJO@comcast.net

Editorial Assistant NANCY J. K. BRAUN

Editorial Board RICHARD C. BANKS
KATHY G. BEAL
JACK CLINTON EITNIEAR
SARA J. OYLER-McCANCE

Review Editor MARY GUSTAFSON
Texas Parks and Wildlife Department
2800 South Bentsen Palm Drive
Mission, TX 78572, USA
E-mail: WilsonBookReview@aolcom

GUIDELINES FOR AUTHORS

Please consult the detailed "Guidelines for Authors" found on the Wilson Ornithological Society web site (http://www.wilsonsociety.org). All manuscript submissions and revisions should be sent to Clait E. Braun, Editor, *The Wilson Journal of Ornithology*, 5572 North Ventana Vista Road, Tucson, AZ 85750-7204, USA. *The Wilson Journal of Ornithology* office and fax telephone number are (520) 529-0365. The e-mail address is TWilsonJO@comcast.net.

NOTICE OF CHANGE OF ADDRESS

Notify the Society immediately if your address changes. Send your complete new address to Ornithological Societies of North America, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

The permanent mailing address of the Wilson Ornithological Society is: %The Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109. Persons having business with any of the officers may address them at their various addresses given on the inside of the front cover, and all matters pertaining to the journal should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Timothy J. O'Connell, Department of Natural Resource Ecology and Management, Oklahoma State University, 205 Life Sciences West, Stillwater, OK 74078; e-mail: oconnet@okstate.edu

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution. The fund will be administered by the Library Committee. Robert Payne, University of Michigan, is Chairman of the Committee. The Library currently receives over 200 periodicals as gifts and in exchange for *The Wilson Journal of Ornithology*. For information on the Library and our holdings, see the Society's web page at http://www.wilsonsociety.org. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: Josselyn Van Tyne Memorial Library, Museum of Zoology, The University of Michigan, 1109 Geddes Avenue, Ann Arbor, MI 48109-1079, USA. Contributions to the New Book Fund should be sent to the Treasurer.

This issue of *The Wilson Journal of Ornithology* was published on 28 May 2008.

Continued from outside back cover

378 Gender identification of Caspian Terns using external morphology and discriminant function analysis
Joshua T. Ackerman, John Y. Takekawa, Jill D. Bluso, Julie L. Yee, and Collin A. Eagles-Smith

384 Effects of traffic noise on auditory surveys of urban White-winged Doves
Jeffrey B. Breeden, Fidel Hernández, Ralph L. Bingham, Nova J. Silvy, and Gary L. Waggerman

Short Communications

390 Specimen shrinkage in Cinnamon Teal
Robert E. Wilson and Kevin G. McCracken

393 Breeding range extension of the Coastal Plain Swamp Sparrow
Bryan D. Watts, Michael D. Wilson, Fletcher M. Smith, Barton J. Paxton, and J. Bill Williams

395 Polyandry and sex ratio in the Song Sparrow
Michael H. Janssen, Peter Arcese, Mark S. Sloan, and Kelly J. Jewell

398 Novel courtship behavior in the Little Greenbul (*Andropadus virens*)
Alexander N. G. Kirschel

401 A recording of a Type B song of the Yellow-throated Warbler
Bailey D. McKay

404 Substrate and vegetation selection by nesting Piping Plovers
Jonathan B. Cohen, Elizabeth H. Wunker, and James D. Fraser

407 Nest site selection by a male Black-capped Vireo
Andrew J. Campomizzi, Shannon L. Farrell, and Jerrod A. Butcher

409 Nests of Black-throated Green Warblers in tree cavities
Douglas C. Tozer

413 Nests and fledglings of the Red-ruffed Fruitcrow (*Pyroderus scutatus*)
Mercival R. Francisco, Paulo R. R. Oliveira Jr., and Vitor O. Lunardi

416 Palila (*Loxioides bailleui*) fledgling fed by Hawai'i 'Amakihi (*Hemignathus virens*)
Chris Farmer, Bridget A. Frederick, Paul C. Banko, Robert M. Stephens, and Carter W. Snow

419 Adoption: adaptation or reproductive error in Eastern Bluebirds?
Daniel P. Wetzel and C. Ray Chandler

422 An intraspecific killing in adult Pacific Reef Egrets (*Egretta sacra*)
Christa Beckmann

425 **Ornithological Literature**
Compiled by Mary Gustafson

The Wilson Journal of Ornithology

(formerly *The Wilson Bulletin*)

Volume 120, Number 2 CONTENTS June 2008

Major Articles

239 New insight to old hypotheses: Ruffed Grouse population cycles
Guthrie S. Zimmerman, Rick R. Horton, Daniel R. Dessecker, and R. J. Gutiérrez

248 Communal calling and prospecting by Black-headed Trogons (*Trogon melanocephalus*)
Christina Riehl

256 Song variation in Buff-breasted Flycatchers (*Empidonax fulvifrons*)
M. Ross Lein

268 Phylogenetic relationship and song differences between closely related Bush Warblers (*Cettia seebohmi* and *C. diphone*)
Shoji Hamao, Maria J. S. Veluz, Takema Saitoh, and Isao Nishiumi

277 Autumn stopover near the Gulf of Honduras by Nearctic-Neotropic migrants
Andrew B. Johnson and Kevin Winker

286 Numbers of migratory birds stopping over in New Orleans, Louisiana, USA in relation to weather
Peter H. Yaukey and Shawn C. Powell

296 Mass changes of migratory landbirds during stopovers in a New York City park
Chad L. Seewagen and Eric J. Slayton

304 Migration of Florida sub-adult Bald Eagles
Elizabeth K. Mojica, J. Michael Meyers, Brian A. Millsap, and Katherin L. Haley

311 Wetland features that influence occupancy by the endangered Hawaiian Duck
Kimberly J. Uyehara, Andrew Engilis Jr., and Bruce D. Dugger

320 Habitat features associated with Barrow's Goldeneye breeding in eastern Canada
Michel Robert, Bruno Drolet, and Jean-Pierre L. Savard

331 Distribution, abundance, and nest-site characteristics of Black Swifts in the southern Rocky Mountains of Colorado and New Mexico
Richard G. Levad, Kim M. Potter, Christopher W. Shultz, Carolyn Gunn, and Joseph G. Doerr

339 Nest reuse by Vermilion Flycatchers in Texas
Kevin S. Ellison

345 Natural history and breeding biology of the Rusty-breasted Antpitta (*Grallaricula ferrugineipectus*)
Alina M. Niklison, Juan I. Areta, Roman A. Ruggera, Karie L. Decker, Carlos Bosque, and Thomas E. Martin

353 Foraging ecology of parrots in a modified landscape: seasonal trends and introduced species
Greg D. Matuzak, M. Bernadette Bezy, and Donald J. Brightsmith

366 The signal function of a melanin-based plumage ornament in Golden-winged Warblers
Emily Anne McKinnon and Raleigh J. Robertson

371 Factors influencing fidelity of House Finches to a feeding station
Andrew K. Davis

Continued on inside back cover

WIL
8424

The Wilson Journal of Ornithology

Volume 120, Number 3, September 2008

MCZ
LIBRARY
MAY 19 2009
HARVARD
UNIVERSITY

Published by the
Wilson Ornithological Society

THE WILSON ORNITHOLOGICAL SOCIETY
FOUNDED 3 DECEMBER 1888
Named after ALEXANDER WILSON, the first American ornithologist.

President—James D. Rising, Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada; e-mail: rising@zoo.utoronto.ca

First Vice-President—E. Dale Kennedy, Biology Department, Albion College, Albion, MI 49224, USA; e-mail: dkennedy@albion.edu

Second Vice-President—Robert C. Beason, USDA, Wildlife Services, 6100 Columbus Avenue, Sandusky, OH 44870, USA; e-mail: beason@netzero.com

Editor—Clait E. Braun, 5572 North Ventana Vista Road, Tucson, AZ 85750, USA; e-mail: TWILSONJO@comcast.net

Secretary—John A. Smallwood, Department of Biology and Molecular Biology, Montclair State University, Montclair, NJ 07043, USA; e-mail: smallwoodj@montclair.edu

Treasurer—Melinda M. Clark, 52684 Highland Drive, South Bend, IN 46635, USA; e-mail: MClark@tcservices.biz

Elected Council Members—Carla J. Dove, Greg H. Farley, and Mia R. Revels (terms expire 2009); Rebecca Holberton, Robert S. Mulvihill, and Timothy O'Connell (terms expire 2010); Jameson F. Chace, Sara R. Morris, and Margaret A. Voss (terms expire 2011).

Membership dues per calendar year are: Active, $21.00; Student, $15.00; Family, $25.00; Sustaining, $30.00; Life memberships, $1,000.00 (payable in four installments).

The Wilson Journal of Ornithology is sent to all members not in arrears for dues.

THE WILSON JOURNAL OF ORNITHOLOGY
(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

All articles and communications for publications should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, MI 48109, USA.

Subscriptions, changes of address, and claims for undelivered copies should be sent to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710, USA. Phone: (254) 399-9636; e-mail: business@osnabirds.org. Back issues or single copies are available for $12.00 each. Most back issues of the journal are available and may be ordered from OSNA. Special prices will be quoted for quantity orders. All issues of the journal published before 2000 are accessible on a free web site at the University of New Mexico library (http://elibrary.unm.edu/sora/). The site is fully searchable, and full-text reproductions of all papers (including illustrations) are available as either PDF or DjVu files.

© Copyright 2008 by the Wilson Ornithological Society
Printed by Allen Press, Inc., Lawrence, KS 66044, U.S.A.

COVER: Wilson's Phalaropes (*Phalaropus tricolor*). Illustration by Robin Corcoran.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

MCZ
LIBRARY
MAY 19 2009
HARVARD
UNIVERSITY

FRONTISPIECE. Analysis of microsatellite DNA suggests that substantial mixing of breeding populations of Swainson's Warbler (*Limnothlypis swainsonii*) may occur in wintering areas in Mexico and Jamaica. Painting by Daniel F. Lane.

The Wilson Journal *of Ornithology*

Published by the Wilson Ornithological Society

VOL. 120, NO. 3 September 2008 PAGES 433–666

The Wilson Journal of Ornithology 120(3):433–445, 2008

GENETIC STRUCTURE OF BREEDING AND WINTERING POPULATIONS OF SWAINSON'S WARBLER

KEVIN WINKER[1,2,3] AND GARY R. GRAVES[1]

ABSTRACT.—Swainson's Warbler (*Limnothlypis swainsonii*) is a species of conservation concern because of its small wintering range in the Caribbean Basin, relatively low population densities, and habitat fragmentation in its core breeding range in the southeastern United States. We investigated microsatellite DNA variation among 11 breeding populations from eastern Texas to Virginia and two populations from wintering areas in Jamaica and Mexico. Analyses of six polymorphic loci indicated a moderate level of gene flow among breeding populations, relatively small effective population sizes (<200 individuals in each sampled population), and subtle population variation. We detected no evidence of population bottlenecks in breeding or wintering populations. Bayesian assignment tests suggested that substantial mixing of breeding populations may occur in wintering areas. Genetic differences between the Mexican and Jamaican populations indicate they may be drawn from different subsets of breeding populations. Patterns of genetic variation among breeding and wintering populations suggest a network of local and regional conservation programs may be necessary to maintain genetic diversity in Swainson's Warbler. *Received 4 May 2007. Accepted 17 December 2007.*

Genetic differentiation in migratory species is often associated with migratory divides where populations that winter in different regions meet during the breeding season in parapatric contact zones (Salomonsen 1955). Studies of *Sylvia* warblers (Sylviidae) in Europe have demonstrated that migratory behaviors can have a strong genetic basis and can evolve rapidly (Berthold and Querner 1981; Helbig 1991, 1996; Berthold 2003; Bearhop et al. 2005). Experimental crosses between populations that winter in different regions produced offspring that exhibited intermediate degrees of migratory orientation and restlessness. Helbig (1991) suggested that hybrids between populations of Eurasian Blackcap (*Sylvia atricapilla*) from opposite sides of the migratory divide would be selected against, because they would probably attempt to migrate across the Mediterranean and end in the uninhabitable expanses of the Sahara Desert. This example suggests a plausible mechanism for maintenance of genetic structure in breeding populations of migratory species that winter in different areas (allohiemy).

Swainson's Warbler (*Limnothlypis swainsonii*) is a sparsely-distributed wood warbler

[1] Department of Vertebrate Zoology, MRC-116, and Laboratory of Molecular Systematics, National Museum of Natural History, Smithsonian Institution, P. O. Box 37012, Washington, D.C. 20013, USA.

[2] Current address: University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775, USA.

[3] Corresponding author; e-mail: ffksw@uaf.edu

(Parulidae) that breeds in the unglaciated southeastern United States and winters in the Caribbean Basin (Meanley 1971; Brown and Dickson 1994; Graves 2001, 2002). Geographic variation in plumage color is subtle and the species is currently regarded as monotypic (Brown and Dickson 1994). Although locally common, Swainson's Warbler has been ranked as one of the most vulnerable breeding songbirds in the southeastern United States because of habitat fragmentation, relatively low population densities, and a small disjunct wintering range (Morse 1989, Terborgh 1989, Hunter et al. 1993, Rappole 1995). Most contemporary breeding populations occur in second-growth forest on alluvial soils in the Mississippi Valley and on the coastal plain from eastern Texas to southeastern Virginia (Graves 1998, 2001, 2002). The nonbreeding distribution is poorly known (Brown and Dickson 1994, Graves 1996), but the primary wintering areas appear to be in Cuba (Kirkconnell et al. 1996), Jamaica (Graves 1996), and in humid forests of mainland Middle America from Veracruz to Tabasco in Mexico (Winker et al. 1992, Winker et al. 1999b) and in Belize (K. Winker, unpubl. data).

Winker et al. (2000) compared allozyme variation at 26 loci among five breeding populations of Swainson's Warbler. Allele frequencies at five loci indicated modest population structure, chiefly between samples in the Mississippi Valley from Arkansas and populations on the coastal plain from Louisiana to Virginia; patterns of genetic variation were inconsistent with an isolation-by-distance model. It was hypothesized the observed population structure was due to genetic drift due to the absence of barriers to gene flow in the contemporary landscape. Alternatively, genetic structuring could be influenced by the warbler's divided wintering range (Greater Antilles vs. mainland Middle America). If migratory behavior is under genetic control in this nocturnally migrating species, interbreeding between populations that winter on the mainland and those that winter in the Greater Antilles might produce offspring that end their migrations over open water in the Caribbean or in the Gulf of Mexico.

We investigated allelic variation at six polymorphic microsatellite loci in 11 breeding populations of Swainson's Warbler sampled from eastern Texas to Virginia and two populations from wintering areas in Jamaica and Mexico. We had three principal objectives: (1) characterize microsatellite diversity within breeding and wintering populations, (2) examine the evidence for mixing of breeding populations on wintering areas, and (3) contrast microsatellite and allozyme variation in the subset of breeding populations studied by Winker et al. (2000).

METHODS

Data Collection.—Swainson's Warblers are territorial in breeding (Meanley 1971) and wintering areas (Graves 1996); they are also monogamous, although polygyny may occur (Graves 1992), and pairing occurs in breeding areas. We obtained tissue samples from 205 territorial males from breeding locations between 27 April and 31 May (1986–1996) in the southeastern United States (Fig. 1) under state and national permits: Sulphur River, Texas (TX1: $n = 17$); Sam Houston National Forest, Texas (TX2: $n = 20$); Atchafalaya River, Louisiana (LA1: $n = 22$); Tensas River, Louisiana (LA2: $n = 10$); Homochitto River, Mississippi (MS1: $n = 20$); Little Sunflower River, Mississippi (MS2: $n = 10$); White and Mississippi rivers, Arkansas (AR: $n = 20$); Apalachicola River, Florida (FL: $n = 24$); Ocmulgee River, Georgia (GA: $n = 20$); Cooper and Santee rivers, South Carolina (SC: $n = 21$); and the Great Dismal Swamp, Virginia, and Chowan River, North Carolina (VA: $n = 21$). These samples nearly span the latitudinal and longitudinal distribution of the core breeding range (Graves 2002). Individuals from five population samples (LA1, AR, FL, SC, and VA) were previously assayed in the allozyme study of Winker et al. (2000). Genetic samples from the wintering range were obtained in Veracruz ($n = 25$) and Tabasco ($n = 1$) in southern Mexico (MEX) and in the Blue Mountains of Jamaica (JAM: $n = 19$; Fig. 1). Voucher specimens (except for Jamaican samples, for which only blood was obtained) are housed in the National Museum of Natural History (Smithsonian Institution), Bell Museum of Natural History (University of Minnesota), and the Coleccion Nacional de Aves (Universidad Nacional Autonoma de Mexico).

Genomic DNA was extracted from body

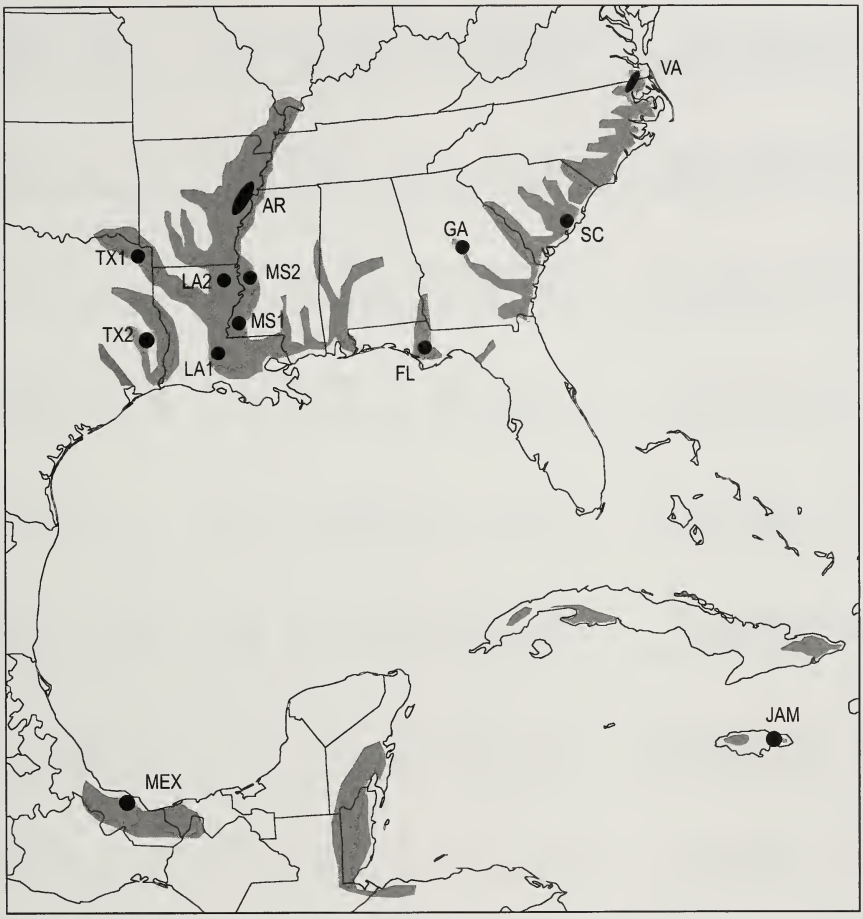


FIG. 1. Sampling localities within the principal breeding and wintering ranges of Swainson's Warbler (after Graves 2002).

tissues or from small pieces of museum skins using a diatomaceous earth/guanidine thiocyanate extraction protocol (Carter and Milton 1993) and diluted to 20 ng/μL for amplification of microsatellite loci developed for this species by Winker et al. (1999a). Extractions and amplifications were conducted in a PCR-free laboratory. All amplification batches included negative controls. Individuals were randomized across extractions, amplifications, and gel runs. Fragments were generated using dye-labeled primers and visualized on an ABI 373A automated sequencer. Fragment size was measured using an internal size standard (350 TAMRA) and GeneScan software (both from Applied Biosystems Inc., Foster City, CA, USA). All electropherograms were examined manually, allele scoring was done without reference to source population, and results were not sorted to population until completion of the study.

Analyses.—Basic statistics of allelic frequencies, genetic distance measures between populations, allelic diversity, and expected and observed heterozygosities were calculated using the computer programs BIOSYS-1 and GDA version 1.0 (Swofford and Selander 1981, Lewis and Zaykin 1999). Tests for Hardy-Weinberg (H-W) equilibrium, allelic heterogeneity, levels of population structure, and differences between population pairs were performed using GENEPOP version 3.1d (Raymond and Rousset 1995). Levels of population structure are given using the θ of Weir and Cockerham (1984), which is an unbiased estimator of traditional F_{ST}. We used CER-

TABLE 1. Allele frequencies for six microsatellite loci among 11 breeding and two wintering populations of Swainson's Warbler (n = 250).

Locus (allele sizes)	Population (n)												
	TX1 (17)	TX2 (20)	LA1 (22)	MS1 (20)	LA2 (10)	MS2 (10)	AR (20)	FL (24)	GA (20)	SC (21)	VA (21)	MEX[a] (26)	JAM (19)
*Lswμ*14 (184–200)													
1	0.029	0	0	0.025	0	0	0.05	0.021	0	0.071	0.048	0.02	0.132
2	0.118	0	0.091	0.05	0	0	0	0.021	0.025	0	0	0.02	0.026
3	0.294	0.3	0.182	0.3	0.4	0.55	0.25	0.354	0.375	0.286	0.262	0.38	0.211
4	0	0	0	0.025	0	0	0.025	0.063	0	0	0	0	0
5	0.235	0.35	0.432	0.425	0.3	0.4	0.425	0.354	0.325	0.357	0.5	0.4	0.342
6	0.324	0.35	0.273	0.175	0.25	0.05	0.225	0.188	0.25	0.286	0.167	0.18	0.289
7	0	0	0.023	0	0	0	0.025	0	0.025	0	0.024	0	0
8	0	0	0	0	0.05	0	0	0	0	0	0	0	0
*Lswμ*18 (227–275)													
1	0	0.025	0	0	0	0	0	0	0	0	0	0	0
2	0.118	0.2	0.182	0.2	0.2	0.3	0.075	0.188	0.225	0.143	0.286	0.28	0.316
3	0.059	0.2	0.159	0.2	0.2	0.1	0.275	0.125	0.15	0.31	0.119	0.14	0.184
4	0.294	0.1	0.182	0.175	0.2	0.1	0.2	0.146	0.25	0.095	0.048	0.18	0.132
5	0.118	0.1	0.227	0.05	0.05	0.15	0.075	0.188	0.1	0.119	0.286	0.1	0.079
6	0.088	0.125	0.023	0.125	0.1	0.15	0.125	0.188	0.075	0.143	0.095	0.18	0.079
7	0.118	0.1	0.068	0.175	0	0.1	0.175	0.063	0.15	0.167	0.143	0.08	0.105
8	0.059	0.1	0.091	0.05	0.2	0.05	0.075	0.042	0.025	0	0	0.02	0
9	0.088	0	0.045	0.025	0	0	0	0.021	0	0	0.024	0	0.053
10	0.059	0.025	0.023	0	0	0	0	0	0.025	0.024	0	0	0
11	0	0	0	0	0.05	0.05	0	0	0	0	0	0	0
12	0	0.025	0	0	0	0	0	0	0	0	0	0.02	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0.026
14	0	0	0	0	0	0	0	0.021	0	0	0	0	0
15	0	0	0	0	0	0	0	0.021	0	0	0	0	0.026
*Lswμ*3 (256–290)													
1	0.029	0.025	0.045	0.075	0.2	0.05	0.05	0.042	0	0.024	0.095	0.08	0
2	0	0	0	0	0	0	0	0.021	0	0	0	0	0
3	0	0.025	0.023	0.025	0	0	0	0	0	0	0	0	0.026
4	0.029	0	0.023	0	0	0	0.025	0	0	0	0	0	0
5	0	0	0	0	0	0	0.025	0	0	0.024	0	0	0
6	0.5	0.45	0.5	0.475	0.35	0.55	0.5	0.438	0.475	0.429	0.5	0.58	0.605
7	0.118	0.125	0.068	0.125	0.2	0.05	0.1	0.146	0.175	0.143	0.095	0.02	0.053
8	0.118	0.075	0.136	0.075	0.05	0.15	0.075	0.125	0.175	0.167	0.19	0.12	0.053
9	0	0.125	0.023	0.05	0.15	0	0.125	0.083	0.05	0.024	0	0.1	0.105
10	0.029	0.05	0.068	0.05	0	0.15	0.025	0.083	0.075	0.071	0.048	0.06	0.105
11	0.088	0.025	0.023	0.025	0	0	0	0	0	0.024	0.024	0.02	0.026

TABLE 1. Continued.

Locus (allele sizes)	Population (*n*)												
	TX1 (17)	TX2 (20)	LA1 (22)	MS1 (20)	LA2 (10)	MS2 (10)	AR (20)	FL (24)	GA (20)	SC (21)	VA (21)	MEX[a] (26)	JAM (19)
12	0	0.05	0.023	0.025	0	0	0	0	0	0.048	0.024	0	0
13	0.059	0.05	0.023	0	0.05	0.05	0	0.021	0.025	0.024	0.024	0.02	0
14	0	0	0.023	0.025	0	0	0.025	0	0.025	0	0	0	0.026
15	0.029	0	0	0.025	0	0	0.025	0.042	0	0.024	0	0	0
16	0	0	0.023	0.025	0	0	0.025	0	0	0	0	0	0
*Lswμ*5B (215–247)													
1	0	0	0	0	0.05	0.05	0	0	0	0	0	0.038	0
2	0.147	0.025	0.045	0.075	0.15	0.05	0	0	0.025	0	0.024	0.038	0
3	0.471	0.575	0.455	0.425	0.35	0.5	0.55	0.479	0.65	0.476	0.167	0.404	0.395
4	0	0	0.023	0	0	0	0	0	0	0	0	0.019	0
5	0.294	0.175	0.318	0.275	0.35	0.2	0.1	0.271	0.225	0.405	0.548	0.308	0.342
6	0.059	0.075	0.091	0.15	0.1	0.15	0.225	0.125	0.05	0.024	0.048	0.096	0.053
7	0.029	0.15	0.045	0.075	0	0.05	0.125	0.083	0.025	0.071	0.214	0.096	0.105
8	0	0	0	0	0	0	0	0.021	0.025	0	0	0	0.079
9	0	0	0	0	0	0	0	0	0	0	0	0	0.026
10	0	0	0	0	0	0	0	0.021	0	0	0	0	0
11	0	0	0.023	0	0	0	0	0	0	0.024	0	0	0
*Lswμ*9 (109–121)													
1	0	0	0	0	0	0	0	0	0.025	0.024	0	0	0.026
2	0	0	0	0	0	0	0	0.042	0	0	0.024	0	0
3	0.618	0.825	0.727	0.625	0.6	0.65	0.825	0.708	0.675	0.833	0.786	0.577	0.842
4	0.382	0.175	0.25	0.35	0.4	0.35	0.175	0.25	0.3	0.143	0.19	0.423	0.132
5	0	0	0.023	0.025	0	0	0	0	0	0	0	0	0
*Lswμ*19 (168–196)													
1	0	0	0	0	0	0	0	0	0	0	0	0.019	0
2	0	0	0	0	0	0	0	0	0	0	0	0.019	0
3	0.118	0.2	0.205	0.175	0.15	0.25	0.05	0.167	0.225	0.119	0.262	0.231	0.342
4	0.059	0.2	0.114	0.175	0.2	0.15	0.2	0.125	0.125	0.333	0.119	0.173	0.158
5	0.294	0.125	0.227	0.175	0.3	0.15	0.275	0.188	0.25	0.095	0.19	0.212	0.237
6	0.118	0.2	0.182	0.1	0.05	0.15	0.15	0.146	0.125	0.167	0.167	0.154	0.053
7	0.147	0.1	0.114	0.25	0.1	0.1	0.2	0.25	0.125	0.214	0.214	0.135	0.079
8	0.088	0.1	0.091	0.05	0.1	0.15	0.1	0.063	0.125	0.048	0.024	0.019	0.079
9	0.118	0.025	0.045	0.075	0.1	0	0.025	0.063	0	0	0	0.038	0.053
10	0.059	0.025	0.023	0	0	0	0	0	0.025	0	0.024	0	0
11	0	0	0	0	0	0.05	0	0	0	0.024	0	0	0
12	0	0.025	0	0	0	0	0	0	0	0	0	0	0

[a] Three individuals could not be scored at one locus each and $n = 25$ at loci 14, 18, and 3.

VUS version 1.0 (Marshall et al. 1998) to infer frequencies of null alleles. We used analysis of covariance (ANCOVA) to evaluate population variability in allelic diversity. The relationship between genetic and geographic distances among populations was assessed with Mantel and permutation tests using NTSYS-pc version 1.50 (Rohlf 1988). We examined geographic subsets of the population matrix with Spearman rank correlation coefficients (r_s). Pairwise comparisons of population parameters are not independent, because each population is subjected to multiple contrasts. Therefore, we emphasize the relative strength of the correlative relationship (r_s) between genetic and geographic distances for these populations rather than *P* values.

We used STRUCTURE, version 2 (Pritchard et al. 2000, Falush et al. 2003) to examine how well the predefined populations corresponded to genetic groups (*K*). Individual genotypes in this Bayesian clustering approach are assigned to clusters with Hardy-Weinberg equilibrium and linkage equilibrium achieved within each cluster. A Markov Chain Monte Carlo approach was used to identify the number of clusters (*K*) that are most likely given the observed genotypes. STRUCTURE was used twice for each defined *K* (1–11) after a burn-in of 10^5 iterations, followed by an additional 10^6 iterations on the full breeding area data set (11 populations). No prior information (e.g., on the population of origin of each individual) was used. Admixture and correlations models were used in which individuals can have mixed ancestry, and where the allele frequencies of closely related populations may be correlated. We further refined our analysis of genetic groups (*K*) using the approach of Evanno et al. (2005), which examines the second order rate of change of the log probability of data with respect to the number of clusters. These analyses were based on 20 independent STRUCTURE runs for each *K* under the same conditions of a 10^5 burn-in, plus another 10^6 iterations. A bootstrapped (100 replicate), neighbor-joining tree was developed using SEQBOOT, GENDIST, NEIGHBOR, and CONSENSE in the software package PHYLIP (Felsenstein 1993).

We tested for population bottlenecks using the computer program M (Garza and Williamson 2001). This test calculates the ratio (M) of total alleles to the range of allele sizes within populations. Reduced populations are expected to have a smaller M ratio than populations in mutation-drift equilibrium (Garza and Williamson 2001). Simulations estimating the probability of the observed M ratio used Garza and Williamson's (2001) suggested values for the proportion of one-step mutations (90%) and the average size of non-one-step mutations (Δ_g = 3.5). We used 10,000 replicates for simulations and set θ ($4N_e\mu$) to 1, 10, and 25, values corresponding to equilibrium effective population sizes (N_e) before a bottleneck of 500, 5,000, and 12,500, respectively, at a mutation rate (μ) of 5×10^{-4} (Goldstein and Schlotterer 1999). Population sizes of Swainson's Warbler are unknown, but values of θ well above 1 seem reasonable given our field experience.

Estimates of $4N_e\mu$ were obtained using MIGRATE (Beerli and Felsenstein 2001), where N_e is effective population size and μ is the microsatellite mutation rate. Our estimates of long-term effective population sizes (N_e) were made using a mutation rate (μ) of 5×10^{-4} (Goldstein and Schlötterer 1999). Estimates of levels of gene flow among breeding populations were made using the rare alleles method (Slatkin 1985, Barton and Slatkin 1986, Slatkin and Barton 1989) as implemented in GENEPOP version 3.1d (Raymond and Rousset 1995) and assignment tests; the latter (Cornuet et al. 1999) enable a more direct estimate of gene flow by calculating the likelihood that an individual genotype originated from the population where it was obtained. These tests remove an individual from the sample and compare it with the remainder (Rannala and Mountain 1997, Cornuet et al. 1999) to identify the most likely breeding population of origin for wintering individuals. We used an α of 0.01, a stringency level shown to have high levels of accuracy in assigning populations of origin for dispersing individuals (Berry et al. 2004). We used the Dunn-Sidák correction (Sokal and Rohlf 1995) where appropriate to adjust probabilities for simultaneous statistical tests.

RESULTS

Variability of Microsatellite DNA.—The six microsatellite loci exhibited 5–16 alleles per locus (Table 1). Sixty-seven alleles were de-

TABLE 2. Sample sizes (n), average allelic diversity (A), and expected and observed heterozygosities (H_e and H_o) for six microsatellite loci in breeding and wintering populations of Swainson's Warbler.

Population	n	A	H_e	H_o
Arkansas (AR)	20	6.17	0.676	0.667
Florida (FL)	24	6.83	0.724	0.660
Georgia (GA)	20	6.00	0.687	0.658
Louisiana 1 (LA1)	22	7.50	0.712	0.652
Louisiana 2 (LA2)	10	5.17	0.754	0.750
Mississippi 1 (MS1)	20	6.83	0.734	0.700
Mississippi 2 (MS2)	10	5.33	0.698	0.767
South Carolina (SC)	21	6.17	0.674	0.690
Texas 1 (TX1)	17	6.33	0.733	0.667
Texas 2 (TX2)	20	6.50	0.687	0.725
Virginia (VA)	21	5.83	0.667	0.690
Mexico (MEX)	26	6.50	0.705	0.620
Jamaica (JAM)	19	6.33	0.672	0.684

tected across all loci, ranging from a minimum of 32 detected in the MS2 population (n = 10 individuals) to a maximum of 45 in the LA1 population (n = 22 individuals). Ten alleles were unique to a single population (FL = 3; JAM = 2; LA2 = 1; MEX = 2; TX2 = 2). The number of alleles detected per population was correlated (r^2 = 0.54; $P < 0.005$) with sample size. Populations from localities that drain into the Atlantic Ocean (VA, SC, GA) had significantly lower allelic diversity (ANCOVA, $F_{1,8}$ = 9.57; P = 0.015) than populations from drainages that empty into the Gulf of Mexico after factoring out the effects of sample size (FL, MS1, MS2, LA1, LA2, AR, TX1, TX2; Table 2). An overall heterozygote deficiency (P = 0.011) was caused by loci *Lswμ*5B and *Lswμ*19 (Table 3). Heterozygote deficiency can be caused by a number of factors, including inbreeding, the Wahlund effect, and null alleles. Inferred frequencies for the latter possibility suggested that null alleles were not responsible for the H-W disequilibrium (Table 3).

Population Structure.—Breeding populations had significant but weak structure (θ = 0.0068, $P < 0.00005$; Table 4) where θ is the unbiased estimator for F_{ST}; this was driven by heterogeneous distributions of alleles in loci *Lswμ*5B ($P < 0.00005$) and *Lswμ*18 (P = 0.039; Table 4). The Bayesian assessment of population clusters reflected this weak structure with the highest probabilities of K occurring for 1–7 populations (Fig. 2A). Further

TABLE 3. Exact tests for Hardy-Weinberg equilibrium (P-values; GENEPOP, Raymond and Rousset 1995) and inferred frequencies of null alleles (CERVUS, Marshall et al. 1998).

Locus	P	Null alleles
*Lswμ*14	0.293	0.006
*Lswμ*18	0.185	0.016
*Lswμ*3	0.429	0.011
*Lswμ*5B	0.029	0.045
*Lswμ*9	0.616	0.004
*Lswμ*19	0.035	0.019

testing to identify the true number of genetic clusters (K), performed separately for both breeding and wintering populations, suggested that 2–4 populations are involved (2–4 among breeding populations and 2–3 in the wintering samples), although the peak height of delta K in both sets of analyses suggested a lack of strong signal in the data set (Fig. 2B, C). A bootstrapped distance tree (10,000 replicates) provided little support for any breeding population associations; just two populations formed one supported clade (FL and MS1 supported by 60% of bootstrap replicates; not shown).

Mantel and permutation tests (NTSYS-pc) of the pooled breeding population data set indicated that genetic distance was at best only weakly associated with geographic distance (Z = 0.27, P = 0.11; 10,000 random permutations). However, when population contrasts were partitioned by geographic region, a clearer view of population differentiation

TABLE 4. Allelic heterogeneity and levels of population structure (θ and associated P-values; Weir and Cockerham 1984) among 11 breeding and between two wintering populations of Swainson's Warbler (GENEPOP, Raymond and Rousset 1995).

	Breeding		Wintering	
Locus	θ	P^a	θ	P^a
Lsw:14	0.003	0.122	0.014	0.098
Lsw:18	0.007	0.039	−0.012	0.585
Lsw:3	−0.009	0.924	−0.014	0.455
Lsw:5B	0.034	0.000	−0.012	0.338
Lsw:9	0.012	0.192	0.144	0.004
Lsw:19	−0.001	0.387	−0.005	0.577
Overall	0.007	<0.00005	0.011	0.044

[a] Adjusted α for series of tests on individual loci is 0.0083. An α of 0.05 for exact tests (bottom row) is not adjusted.

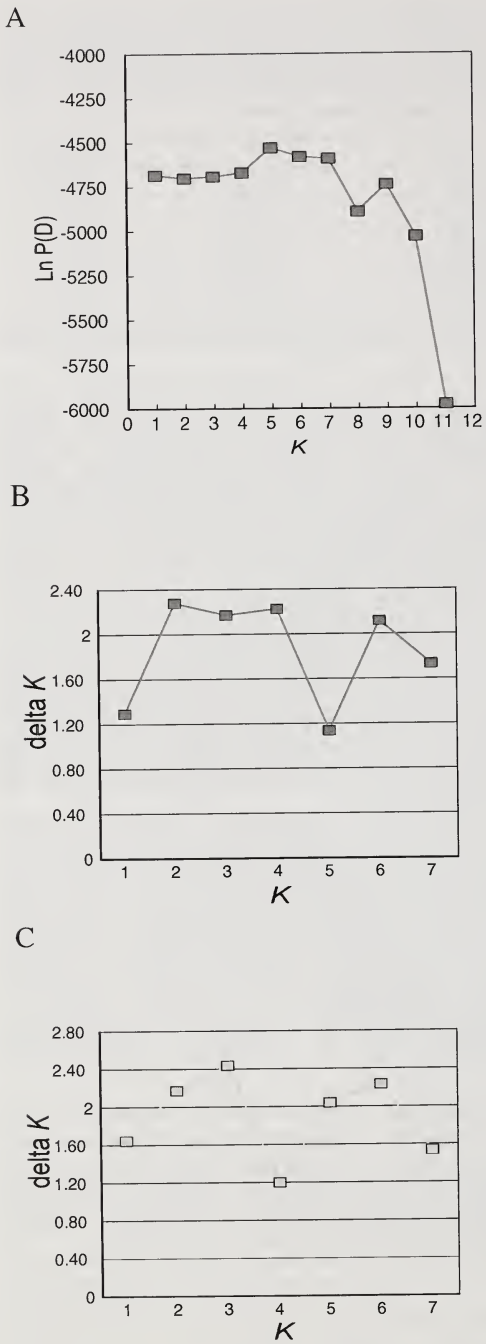


FIG. 2. A. Probabilities, ln P(D), of population samples coming from *K* genetic groups using Bayesian analyses of the full breeding area data set (STRUCTURE Version 2, Pritchard et al. 2000; Falush et al. 2003). The set of 11 breeding populations oversampled the number of actual genetic clusters present, a value that ranges from 1 to 7. The second and third figures show delta *K*, the second order rate of change of ln P(D) in relation to *K* (Evanno et al. 2005), of breeding (B) and wintering (C) populations suggesting that 2–4 genetic clusters are most probable among the 11 sampled breeding populations, and that just 2–3 are most likely represented in the wintering populations (although peak heights and signal in these data sets are low).

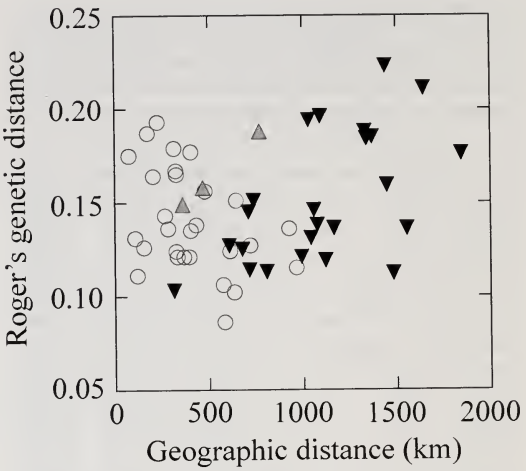


FIG. 3. Rogers' (1972) genetic distance and geographic distance between breeding populations of Swainson's Warbler: (circles) pairwise comparisons between localities that drain into the Gulf of Mexico (TX1, TX2, LA1, LA2, MS1, MS2, AR, FL); (gray triangles) pairwise comparisons between localities that drain into the Atlantic Ocean (GA, SC, VA); (black triangles) pairwise comparisons between Gulf and Atlantic drainage localities.

emerged (Figs. 1, 3). Pairwise comparisons between Gulf populations (n = 28 contrasts) indicated a slightly negative relationship between genetic and geographic distance (r_s = −0.39). The relationship between genetic and geographic distance was substantially weaker (r_s = −0.23) when pairwise comparison was limited to the seven populations from the Mississippi and Sabine river drainages (n = 21 contrasts) of the western Gulf. In contrast, pairwise contrasts (n = 24) between populations from Atlantic drainages with those from Gulf drainages exhibited a markedly positive correlation (r_s = 0.49), suggesting a weak longitudinal trend toward genetic isolation-by-distance. The most geographically isolated population in our survey (VA) also exhibited the greatest average pairwise genetic distance

from other populations. The most centrally located population (FL) also showed the lowest average genetic distance between populations.

Wintering populations exhibited significant but weak structure ($\theta = 0.0111$, $P = 0.044$; Table 4). This was driven largely by locus *Lsw*μ9 ($P = 0.004$; other loci $P > 0.098$; Table 4). The loci responsible for breeding and wintering population structure were different (Table 4).

Allozyme and Microsatellite Comparisons.—We compared genetic distance matrices derived from allozymes and the microsatellite loci examined in this study for five breeding populations (LA1, AR, FL, SC, VA). The null hypothesis that the two matrices were not associated could not be rejected with Mantel and permutations tests ($Z = 0.18$, $P = 0.30$; 10,000 random permutations) indicating the two nuclear genetic marker systems examined for this subset of breeding populations exhibited discordant patterns of differentiation.

Gene Flow.—The rare alleles method, an indirect technique to estimate the number of migrants per generation, inferred $Nm = 9.16$ among breeding populations after correction for sample size (where mean sample size was 18.6 and mean frequency of private alleles $P[1] = 0.026$). Assignment tests, which are more reflective of contemporary gene flow, indicated that three to seven individuals (15–70%) from each breeding population had genotypes that were significantly unlikely to have originated there (averaging 4.4 individuals or 25% per population; Table 5). These values ranged from two to five individuals per population (averaging 3.2 individuals or 18% per population; Table 5) when adjusted for type-I error (Dunn-Sidák test). These numbers were similar in the two wintering populations (averaging 4.5 individuals per population, or 3.5 with the Dunn-Sidák correction; Table 5). The genotypes of three individuals from Florida and single individuals from Mississippi (MS1), South Carolina, and Texas (TX2) could not be assigned to any breeding population (all with $P < 0.00005$). Similarly, two individuals from Jamaica and one from Mexico could not be assigned to any breeding or wintering population. Both the rare alleles method and assignment tests suggested a moderate amount of gene flow among breeding populations ($Nm = 3.2$–9.2).

TABLE 5. Assignment test results comparing genotypes of individuals with genotypic characteristics of the breeding populations from which they were sampled (GeneClass, Cornuet et al. 1999).

Population	*n*	Mean Bayesian probability (± SD)[a]	Genotypes not from sampled population[b]
Arkansas (AR)	20	0.37 ± 0.38	5
Florida (FL)	24	0.34 ± 0.30	5
Georgia (GA)	20	0.32 ± 0.31	3
Louisiana 1 (LA1)	22	0.28 ± 0.29	5
Louisiana 2 (LA2)	10	0.11 ± 0.20	7
Mississippi 1 (MS1)	20	0.29 ± 0.29	4
Mississippi 2 (MS2)	10	0.16 ± 0.27	3
South Carolina (SC)	21	0.31 ± 0.32	3
Texas 1 (TX1)	17	0.23 ± 0.25	4
Texas 2 (TX2)	20	0.32 ± 0.28	5
Virginia (VA)	21	0.38 ± 0.30	4
Mexico (MEX)	26	0.35 ± 0.34	4
Jamaica (JAM)	19	0.32 ± 0.29	5

[a] Averaged Bayesian posterior probabilities of membership among a population's individuals (Rannala and Mountain 1997, Cornuet et al. 1999).
[b] Number of individuals with probabilities of membership from population of origin with $P < 0.01$.

Long-term Population Size.—We obtained estimates of $4N_e\mu$, where N_e is effective population size and μ is the microsatellite mutation rate. These analyses suggested uniformly small long-term effective population sizes (N_e) ranging from a low of 44 (LA2) to a high of 174 (LA1; Table 6). There was no evidence for population genetic bottlenecks in breeding or wintering populations at any of the modeled values of θ (1, 10, and 25; $P > 0.1$), despite these rather low estimates of long-term effective population size.

Evidence of Winter Mixing.—We compared the allelic frequencies of wintering populations from Mexico and Jamaica with those of each of the 11 breeding populations to investigate the genetic relationships between breeding and wintering populations. No genetic differences were found between any pairwise combination of wintering and breeding population when α was adjusted for multiple tests (Table 7). Evidence of geographic segregation of breeding populations in wintering areas remained weak under a less conservative approach (no adjustment of α). Allelic frequencies of the Mexican wintering population were significantly different from those of breeding populations from Arkansas (AR) in the Mis-

TABLE 6. Estimates of $4N_e\mu$ and the 95% confidence interval (following Beerli and Felsenstein 2001) where N_e is effective population size and μ is the mutation rate of microsatellite loci. Subsequent estimates of long-term effective population sizes (N_e est.) and the corresponding 95% confidence intervals are based on a mutation rate of 5×10^{-4} (Goldstein and Schlötterer 1999) and are well below contemporary census sizes of these populations.

Population	$4N_e\mu$	95% CI[a]	N_e est.	95% CI
Arkansas (AR)	0.18	(0.16–0.21)	92	(81–105)
Florida (FL)	0.24	(0.21–0.26)	118	(105–132)
Georgia (GA)	0.17	(0.15–0.20)	86	(75–98)
Louisiana 1 (LA1)	0.35	(0.30–0.41)	174	(150–204)
Louisiana 2 (LA2)	0.09	(0.08–0.10)	44	(38–51)
Mississippi 1 (MS1)	0.16	(0.14–0.18)	80	(71–91)
Mississippi 2 (MS2)	0.09	(0.08–0.11)	45	(39–53)
South Carolina (SC)	0.22	(0.19–0.25)	108	(96–123)
Texas 1 (TX1)	0.14	(0.13–0.16)	71	(63–81)
Texas 2 (TX2)	0.20	(0.18–0.23)	102	(89–117)
Virginia (VA)	0.16	(0.14–0.18)	78	(69–88)
Mexico (MEX)	0.34	(0.30–0.38)	170	(152–192)
Jamaica (JAM)	0.17	(0.15–0.19)	84	(74–96)

[a] Based on multiple runs after initial, random parameter estimates were used to seed additional runs and convergence on similar values was verified.

sissippi Valley and Virginia (VA) and South Carolina (SC) on the Atlantic coastal plain (Table 7). Similarly, allelic frequencies of the Jamaican wintering population were significantly different from those of breeding populations from Louisiana (LA2), Arkansas (AR), Texas 1 (TX1), and Virginia (VA; all $P < 0.02$; Table 7).

We assigned wintering individuals to their most likely breeding population by choosing the highest probability *P*-value from the array of breeding populations. All but two individuals from Mexico and two from Jamaica could be assigned to one of the 11 breeding populations ($P < 0.01$). Of the 24 assignable individuals from Mexico, only Arkansas (AR) and Georgia (GA) were eliminated as likely breeding populations; and among the 16 assignable individuals from Jamaica, only Louisiana (LA2), Mississippi (MS2), and Virginia (VA) were unlikely breeding sources. This suggests that individuals from a substantial number of geographically distinct breeding populations mix in wintering areas in Mexico and Jamaica.

DISCUSSION

The breeding distribution of Swainson's Warbler has decreased significantly during the past century because of deforestation of bot-

TABLE 7. Pairwise comparisons showing genetic similarities and differences between two wintering and 11 breeding populations of Swainson's Warbler (θ and associated *P*-values; GENEPOP).

	Mexico (MEX)		Jamaica (JAM)	
	θ	*P*[a]	θ	*P*[a]
Arkansas (AR)	0.0211	0.0126	0.0200	0.0107
Florida (FL)	−0.0046	0.5485	0.0081	0.1444
Georgia (GA)	0.0004	0.3073	0.0112	0.1641
Louisiana (LA1)	0.0006	0.1796	−0.0007	0.2652
Louisiana (LA2)	−0.0082	0.3890	0.0221	0.0070
Mississippi (MS1)	−0.0122	0.9319	0.0087	0.1468
Mississippi (MS2)	−0.0195	0.9580	0.0163	0.0831
South Carolina (SC)	0.0217	0.0115	0.0117	0.1059
Texas (TX1)	0.0015	0.0645	0.0201	0.0062
Texas (TX2)	0.0125	0.1380	0.0042	0.3184
Virginia (VA)	0.0207	0.0169	0.0173	0.0178

[a] Experiment error held at $\alpha = 0.05$, and adjusted alpha for each series of tests = 0.0045.

tomlands, flood mitigation projects, and forestry practices that minimize early successional habitats (Twedt and Loesch 1999; Graves 2001, 2002). Several populations near the northern periphery of the warbler's breeding range have disappeared in recent decades and many of the remaining populations are isolated. We detected no evidence of genetic bottlenecks in breeding or wintering populations despite relatively small effective population sizes and fragmentation of the warbler's geographic range. However, the lower allelic diversity exhibited among Atlantic-drainage populations and the significant correlation between genetic and geographic distances observed in pairwise comparisons of Gulf-drainage populations with those sampled in Atlantic drainages suggests that subtle population structure exists among breeding populations. Clustering tests further suggested that breeding populations sampled in this study are composed of two to four genetic populations. Whether differentiation is caused by genetic drift, stochastic sampling effects, selection associated with the warbler's disjunct wintering range, or other factors is unknown.

The moderate levels of gene flow among breeding populations revealed by microsatellite data (Nm = 3.2–9.2) were consistent with the results of an earlier survey of allozymes (Winker et al. 2000) in a subset of five populations (Nm = 1.5–11.7). However, spatial patterns of genetic variation revealed by microsatellites and allozymes were discordant, a not uncommon event between molecular marker systems (Allendorf and Seeb 2000). Significant population structure was caused by two microsatellite loci in the present study and three of 16 loci examined in our earlier allozyme study.

Mixing of breeding populations in wintering areas is believed to be a common phenomenon because breeding ranges of most Nearctic-Neotropic migratory songbirds are considerably larger than their wintering ranges (Terborgh 1989). The signal of geographic structure in our microsatellite data is weak, but Bayesian assignment tests imply that at least six breeding populations (TX1, TX2, LA1, MS1, FL, and SC) could have contributed wintering individuals to both the Mexican and Jamaican wintering populations. However, genetic differences between the Mexican and Jamaican populations suggest they are comprised of different subsets of breeding populations.

CONSERVATION IMPLICATIONS

Should breeding populations of Swainson's Warbler be managed as a single conservation unit? Patterns of microsatellite variation among breeding and wintering populations suggest that multi-regional and international efforts will likely be required to maintain the current level of genetic diversity in the species. Implementation of a viable management plan for the species throughout its global range, however, is contingent upon the development of additional genetic markers that can more fully resolve the genetic structure of breeding populations and their distributions during the nonbreeding season. Future field efforts should focus first on obtaining genetic samples from breeding populations in the Appalachian and Ozark mountains and from wintering populations in Cuba and Belize.

ACKNOWLEDGMENTS

The Legacy Resource Management Program of the U.S. Department of Defense (DAMD17-93-J-3073, DACA87-94-H-0012) and the Research Opportunities Fund of the Smithsonian Institution supported this study. Numerous agencies kindly granted permits for the research: Jamaican Conservation and Development Trust; National Resources Conservation Authority (Kingston); USDA Forest Service; U.S. Fish and Wildlife Service; U.S. Department of Defense; Arkansas Game and Fish Commission; Florida Fish and Wildlife Conservation Commission; Georgia Department of Natural Resources; Louisiana Department of Wildlife and Fisheries; Mississippi Department of Wildlife, Fisheries, and Parks; North Carolina Wildlife Resources Commission; South Carolina Department of Natural Resources; Texas Parks and Wildlife Department; and Virginia Department of Game and Inland Fisheries. R. T. Brumfield and T. C. Glenn helped with marker development. R. M. Zink permitted us to sample study skins in the Bell Museum of Natural History. Patricia Escalante P provided additional samples from Mexico. B. K. Schmidt, C. M. Milensky, J. P. Angle, and J. P. Dean assisted with specimen preparation. Francois Rousset provided helpful correspondence on making multiple comparisons. M. J. Braun, R. T. Brumfield, P. O. Lewis, and C. L. Pruett provided helpful comments on an earlier draft.

LITERATURE CITED

Allendorf, F. W. and L. W. Seeb. 2000. Concordance of genetic divergence among sockeye salmon pop-

ulations at allozyme, nuclear DNA, and mitochondrial DNA markers. Evolution 54:640–651.

Barton, N. H. and M. Slatkin. 1986. A quasi-equilibrium theory of the distribution of rare alleles in a subdivided population. Heredity 56:409–415.

Bearhop, S., W. Fiedler, R. W. Furness, S. C. Votier, S. Waldron, J. Newton, G. J. Bowen, P. Berthold, and K. Farnsworth. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. Science 310:502–504.

Beerli, P. and J. Felsenstein. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. Proceedings of the National Academy of Sciences USA 98:4563–4568.

Berry, O., M. D. Tocher, and S. D. Sarre. 2004. Can assignment tests measure dispersal? Molecular Ecology 13:551–561.

Berthold, P. 2003. Genetic basis and evolutionary aspects of bird migration. Advances in the Study of Behavior 33:175–229.

Berthold, P. and U. Querner. 1981. Genetic basis of migratory behavior in European warblers. Science 212:77–79.

Brown, R. E. and J. G. Dickson. 1994. Swainson's Warbler (*Limnothlypis swainsonii*). The birds of North America. Number 126.

Carter, M. J. and I. D. Milton. 1993. An inexpensive and simple method for DNA purification on silica particles. Nucleic Acids Research 21:1044.

Cornuet, J.-M., S. Piry, G. Luikart, A. Estoup, and M. Solignac. 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. Genetics 153: 1989–2000.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611–2620.

Falush, D., M. Stephens, and J. K. Pritchard. 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164:1567–1587.

Felsenstein, J. 1993. PHYLIP (Phylogeny Inference Package) Version 3.5c. Distributed by the author. Department of Genetics, University of Washington, Seattle, USA.

Garza, J. C. and E. G. Williamson. 2001. Detection of reduction in population size using data from microsatellite loci. Molecular Ecology 10:305–318.

Goldstein, D. B. and C. Schlötterer. 1999. Microsatellites: evolution and applications. Oxford University Press, Oxford, United Kingdom.

Graves, G. R. 1992. A case of aggregated nest placement and probable polygyny in Swainson's Warbler. Wilson Bulletin 104:370–373.

Graves, G. R. 1996. Censusing wintering populations of Swainson's Warbler: surveys in the Blue Mountains of Jamaica. Wilson Bulletin 108:94–103.

Graves, G. R. 1998. Stereotyped foraging behavior of the Swainson's Warbler. Journal of Field Ornithology 69:121–127.

Graves, G. R. 2001. Factors governing the distribution of Swainson's Warbler along a hydrological gradient in Great Dismal Swamp. Auk 118:650–664.

Graves, G. R. 2002. Habitat characteristics in the core breeding range of the Swainson's Warbler. Wilson Bulletin 114:210–220.

Helbig, A. J. 1991. SE- and SW-migrating Blackcap (*Sylvia atricapilla*) populations in central Europe: orientation of birds in the contact zone. Journal of Evolutionary Biology 4:657–670.

Helbig, A. J. 1996. Genetic basis, mode of inheritance and evolutionary changes of migratory directions in Palearctic warblers (Aves: Sylviidae). Journal of Experimental Biology 199:49–55.

Hunter, W. C., D. N. Pashley, and R. E. F. Escano. 1993. Neotropical migratory landbird species and their habitats of special concern with the southeast region. Pages 159–171 *in* Status and management of neotropical migratory birds (D. M. Finch and P. W. Stangel, Editors). USDA, Forest Service General Technical Report RM-229. Fort Collins, Colorado, USA.

Kirkconnell, A., G. E. Wallace, and O. H. Garrido. 1996. Notes on the status and behavior of the Swainson's Warbler in Cuba. Wilson Bulletin 108: 175–178.

Lewis, P. O. and D. Zaykin. 1999. Genetic data analysis: computer program for the analysis of allelic data. (www.eeb.uconn.edu/people/plewis/software.php).

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639–655.

Meanley, B. 1971. Natural history of the Swainson's Warbler. North America Fauna 69:1–90.

Morse, D. H. 1989. American warblers: an ecological and behavioral perspective. Harvard University Press, Cambridge, Massachusetts, USA.

Pritchard, J. K., M. Stephens, and P. J. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Rannala, B. and J. L. Mountain. 1997. Detecting immigration by using multilocus genotypes. Proceedings of the National Academy of Sciences USA 94:9197–9201.

Rappole, J. H. 1995. The ecology of migrant birds. Smithsonian Institution Press, Washington, D.C., USA.

Raymond, M. and F. Rousset. 1995. GENEPOP (Version 1.2): a population genetics software for exact tests and ecumenicism. Journal of Heredity 86: 248–249.

Rogers, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics 7:145–153.

Rohlf, F. J. 1988. NTSYS-pc: numerical taxonomy and multivariate analysis system. Exeter Software, Setauket, New York, USA.

Salomonsen, F. 1955. The evolutionary significance of

bird-migration. Det Kongelige Danske Videnskabernes Selskab 22:1–62.

Slatkin, M. 1985. Rare alleles as indicators of gene flow. Evolution 39:53–65.

Slatkin, M. and N. H. Barton. 1989. A comparison of three indirect methods for estimating average levels of gene flow. Evolution 43:1349–1368.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry. Third Edition. W. H. Freeman and Company, New York, USA.

Swofford, D. L. and R. B. Selander. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. Journal of Heredity 72: 281–283.

Terborgh, J. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey, USA.

Twedt, D. J. and C. R. Loesch. 1999. Forest area and distribution in the Mississippi alluvial valley: implications for breeding bird conservation. Journal of Biogeography 26:1215–1224.

Weir, B. S. and C. C. Cockerham. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370.

Winker, K., T. C. Glenn, and G. R. Graves. 1999a. Dinucleotide microsatellite loci in a migratory wood warbler (Parulidae: *Limnothlypis swainsonii*), and amplification among other songbirds. Molecular Ecology 8:1553–1556.

Winker, K., G. R. Graves, and M. J. Braun. 2000. Genetic differentiation among populations of a migratory songbird: *Limnothlypis swainsonii*. Journal of Avian Biology 31:319–328.

Winker, K., S. Arriaga Weiss, P. J. Lourdes Trejo, and P. Escalante 1999b. Notes on the avifauna of Tabasco. Wilson Bulletin 111:229–235.

Winker, K., R. J. Oehlenschlager, M. A. Ramos, R. M. Zink, J. H. Rappole, and D. W. Warner. 1992. Avian distribution and abundance records for the Sierra de Los Tuxtlas, Veracruz, Mexico. Wilson Bulletin 104:699–718.

The Wilson Journal of Ornithology 120(3):446–454, 2008

DOES AGE INFLUENCE TERRITORY SIZE, HABITAT SELECTION, AND REPRODUCTIVE SUCCESS OF MALE CANADA WARBLERS IN CENTRAL NEW HAMPSHIRE?

LEONARD R. REITSMA,[1,2,3] MICHAEL T. HALLWORTH,[1,2] AND PHRED M. BENHAM[2]

ABSTRACT.—The Canada Warbler (*Wilsonia canadensis*) is currently in decline in the northeastern United States and basic demographic parameters remain to be described. We studied marked populations (76 ASYs, 14 SYs, and 2 of unknown age) of Canada Warblers on two study sites from 2003 to 2006. We mapped 92 territories (including males returning in multiple years) of 71 males using handheld GPS and ArcMap. We compared the pairing and fledging success of older and younger males on both sites, a red maple (*Acer rubrum*) swamp and a young forest intensively harvested in 1985 with ~10% residual standing trees used by males as song perch trees. Both sites had a high proportion of ASYs (84% ASY for all territorial males, 77.5% of all males including non-territorial individuals). Both pairing (91%) and fledging (78%) success was comparatively high suggesting these two sites were of high value to this species. A higher proportion of SYs were transients. Pairing success was lower for younger males which established territories, but paired SYs fledged at least one young at a rate comparable to older males. This study corroborates the benefits of age and experience to reproductive performance. The results suggest that both red maple swamps and post-harvest forests with thick subcanopy vegetation and emergent trees provide high quality habitat for breeding Canada Warblers. *Received 11 July 2007. Accepted 12 November 2007.*

Demographic studies are important in understanding the population ecology of a bird species, especially during the breeding season. A bird's age can greatly affect its ability to hold high quality territories, pair, and successfully raise young (e.g., Ficken and Ficken 1966, Holmes et al. 1996). Older age and greater experience of males are often associated with higher reproductive performance. This has been shown for a diversity of bird species from several different families. Mates with older male Great Tits (*Parus major*) laid earlier, fledged more young, and their fledglings survived at higher rates, although age of the male did not affect clutch size (Perrins and McCleery 1985). Age of the European Pied Flycatcher (*Ficedula hypoleuca*) was similarly correlated with laying date and fledgling survivorship, and older males also had greater clutch sizes (Harvey et al. 1985). Nol and Smith (1987) found that older Song Sparrows (*Melospiza melodia*) began breeding earlier and raised more young to independence than younger Song Sparrows.

The effects of age on territory quality and reproductive success have been frequently studied among Parulidae. Habitat features and/or food availability affect individual bird territory quality, which in turn influences territory size, site fidelity, and reproductive success; older males disproportionately occupy higher quality habitat (e.g., Rodenhouse and Holmes 1992). The age of Ovenbirds (*Seiurus aurocapilla*) positively correlates with habitat quality and pairing success. Older males acquire higher quality habitats and pair at higher rates than younger males (Bayne and Hobson 2001). Holmes et al. (1996) found that older Black-throated blue Warblers (*Dendroica caerulescens*) occurred in areas with higher shrub density and fledged significantly more young. Older males also returned at higher rates than yearlings and had significantly smaller territory sizes. Older American Redstart (*Setophaga ruticilla*) males arrive earlier, and pair and fledge young at higher rates than first year males. Older males also relegate first year males to less optimal breeding habitat (Sherry and Holmes 1989). These findings indicate that habitat variables and age may influence breeding success and return rates of warblers.

Understanding the relationship between age and reproductive performance and how age

[1] Plymouth State University, 17 Highland Avenue, Plymouth, NH 03264, USA.

[2] New England Institute for Landscape Ecology, 266 Prospect Hill Road, Canaan, NH 03741, USA.

[3] Corresponding author; e-mail: leonr@plymouth.edu

structure differs among habitats provides the needed tools for management, especially for species with documented declines. Habitat type is not a reliable predictor of reproductive success (Van Horne 1983, Vickery et al. 1992), but demographic patterns among different habitats within a species' distribution indicate age-related effects. Younger birds are often displaced into lower quality habitat where they are incapable of attracting a mate or raising young (e.g., Holmes et al. 1996, Zanette 2001). This is consistent with age-specific models of habitat selection that suggest older birds assert dominance over younger birds and secure the best habitat and, consequently, have higher fitness (e.g., Holmes et al. 1996, Hunt 1996).

This study focused on the Canada Warbler (*Wilsonia canadensis*), a small (10–12 g) Neotropic-Nearctic migrant. The Canada Warbler breeds in areas with high shrub density, such as red maple (*Acer rubrum*) swamps and young upland forest (Titterington et al. 1979, Hagan et al. 1997, Golet et al. 2001). It occurs in both early-successional forest stands and within the deciduous (DeGraaf et al. 1998) and mixed-species understories of mature forests in New Hampshire during the breeding season. The species' population is in a 2.7–4.6% per year decline over the last four decades in the region that includes this study, as estimated from North American Breeding Bird Survey data (Sauer et al. 2005). The reasons for this decline are poorly understood as few studies have been performed at the level of the individual or population. Most studies involving the Canada Warbler have been conducted at the community level, involving censuses in differing habitats. This study compares age-related habitat selection and breeding success in both naturally occurring red maple swamps and young upland forest, clearcut in 1985 with residual tree retention.

The objectives of this study were to examine differences in the habitat characteristics, breeding success, and territory sizes between after-second-year (ASY) and second-year (SY) males within the same breeding population. We predicted these measures will show consistent patterns similar to those documented with other species. Older birds were predicted to have smaller territories, and higher pairing and fledging success consistent with age-based dominance-hierarchical models.

METHODS

Study Site.—This study was conducted in Canaan, New Hampshire (43° 40′ N, 72° 03′ W) on the Canaan Town Forest (40 ha, hereafter referred to as the lower plot) and the adjacent Bear Pond Natural Area (BPNA) (363 ha, hereafter referred to as the upper plot) (Fig. 1). The lower plot is a 40-ha red maple swamp dominated by balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and red maple with interspersed mixed upland forest. The upper plot (all within BPNA) is a 43-ha mixed deciduous upland forest, which was heavily harvested in 1985. Young regrowth dominated the harvest zone; remnant nonmerchantable trees emerge from the regenerating layer as scattered individuals and in clumps. Trees (≥8.0 cm dbh) of the upper plot were dominated by red maple, balsam fir, eastern hemlock (*Tsuga canadensis*), red spruce, and big-toothed aspen (*Populus grandidentata*). Balsam fir dominated the smallest size class of shrubs and saplings (<2.5 cm dbh) on the upper plot followed by *Ilex* and *Viburnum* spp., white birch (*Betula papyrifera*), and red maple.

Characterizing Male Territories.—Seventy-one territorial males were captured from 2003 to 2006 using playback of songs and calls. All birds were uniquely color-banded. Birds were assigned to age classes following plumage characteristics, i.e., molt limits of the outer primary coverts, and boldness and extent of the necklace (Rappole 1983, Pyle 1997). Male territories were mapped from 27 May to 10 July each year. Every territorial male was observed for six 30-min periods. The bird's location was recorded during each observation period with a Global Positioning System (GPS) unit at 5-min intervals. Every territorial male was observed for six observation bouts resulting in a minimum of 42 data points. All birds were followed between dawn and 0930 hrs EDT. We used Adaptive Kernel (ADK) to construct territory boundaries (95% ADK) and the "core" territory areas (50% ADK) from each individual's location data (Barg et al. 2005). Territory boundaries and sizes were calculated using CALHOME home range analysis program (Kie et al. 1994).

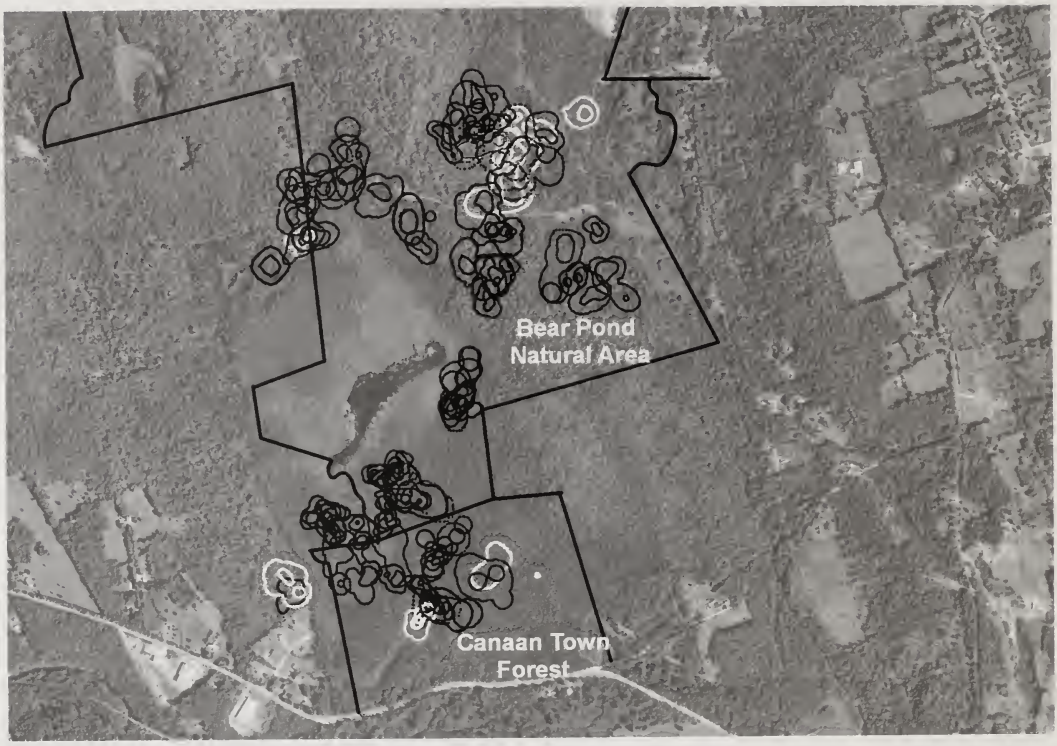


FIG. 1. Canada Warbler territories during 2003–2006 in central New Hampshire used to compare reproductive performance. After-second-year (ASY) male territories are shown in black and second-year (SY) male territories are shown in white. Each territory is the result of an adaptive kernel (ADK) analysis using GPS locations taken during 30-min observation bouts.

Measuring Reproductive Success.—Pairing and fledging success were documented for each male within observation bouts. A male was considered paired if a female was repeatedly detected within his territory. Males singing from high perches throughout the breeding season with no female detected were considered unpaired. A nest on a male's territory was considered successful if at least one fledgling was seen (Howlett and Stutchbury 2003), or if males and females concurrently delivered food to multiple areas within the territory.

Vegetation Sampling.—Minimum convex polygons (MCP) were calculated using CALHOME (Kie et al. 1994) to position up to four vegetation sampling locations on each male's territory. We used MCPs to be consistent with data collected across all years. Only males with the full set of six complete observation bouts were used in vegetation analyses in 2005 and 2006 (n = 39 male territories). Ninety-two male territories had a complete set of six observation bouts from 2003 to 2006 and were used for comparing reproductive success. All vegetation characteristics were quantified using a modification of the Breeding Biology Research and Monitoring [BBIRD] protocol (Martin and Conway 1994). Thirty-nine sets of vegetation plots, each set consisting of 4 subplots, were placed within territories. The position of subplots followed the BBIRD protocol except on territories where subplots had to be shifted to either remain more than 50% within territory boundaries or include actual locations of birds within their territories. If a subplot contained fewer than two observation points or was more than 50% outside of the polygon, it was shifted the least distance possible to meet the criteria. Thirty-two sets of non-territory plots were created using a random number generator and randomly placed in habitat that was not occupied.

We characterized a song perch tree as any

tree that emerged at least 3 m above the surrounding canopy with a radius of >5 m that was not overlapping with the surrounding canopy. These perch sites were presumed to provide high visibility and maximize the distance during singing at which a song may be heard by conspecifics. The density of the shrub foliage was quantified using a pole (2.5 m long and 2.5 cm diameter) marked at half-meter intervals. We recorded the plant species and number of times a branch or leaf touched the pole within each half-meter interval. The pole was placed 1 m from the center of the plot in each of the four cardinal directions. All four subplots for each territory or non-territory analog were averaged for analysis to best approximate the habitat in the area sampled.

Statistical Analyses.—Chi-square analyses were used to compare pairing and fledging success between older (ASY) and younger (SY) males. Fisher's exact test was used to compare age classes of males in 2005 and 2006 on both plots. Wilcoxon signed rank analysis was used, due to non-normal distributions, to compare the territory and core area sizes of older and younger males that had a complete set of observation bouts (42 location points), and to analyze differences in habitat characteristics between the two age classes. Habitat comparisons were made by combining plots to maximize sample size within each age class (Bonferroni adjustments were made for habitat characteristics that were not considered independent, shrub stems: $P < 0.01$, shrub foliage density: $P < 0.01$, tree stems: $P < 0.0083$). We also analyzed age class differences in habitat characteristics within each plot and made the same Bonferroni adjustments for multiple comparisons of variables that were not considered independent.

RESULTS

Ninety-two territories of 71 males over 4 years (2003–2006) were mapped with a complete set of six 30-min observation bouts including 17 males mapped in two consecutive years and four males mapped in three consecutive years. Ninety-three percent of territorial males (66 of 71) were banded. Territories of these marked individuals surrounded unbanded territorial males, making it possible to accurately map the five unmarked individuals. Of the 92 male territories mapped over 4

TABLE 1. Average (± SE) territory sizes and core areas (± SE) of ASY and SY males in each year calculated by adaptive kernel analysis. These data were based exclusively on males for which a full set of location data points were obtained ($n = 90$). Neither the 4-year average territory sizes nor core areas differed significantly between ASY and SY males.

	Year							
	2003		2004		2005		2006	
Age	Terr.	Core	Terr.	Core	Terr.	Core	Terr.	Core
ASY	1.12 (0.238)	0.249 (0.065)	0.67 (0.140)	0.107 (0.017)	1.11 (0.179)	0.152 (0.036)	1.18 (0.113)	0.232 (0.024)
SY	1.16 One SY	0.150	No SYs in 2004		1.36 (0.165)	0.286 (0.037)	1.27 (0.227)	0.203 (0.041)

TABLE 2. Number (%) of each Canada Warbler age class on each of two plots for each year in west-central New Hampshire during 2003 to 2006.

	All males				Territorial males ≥30 observations			
	2005		2006		2005		2006	
Age	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
ASY	11 (52)	14 (82)	24 (83)	17 (77)	9 (64)	13 (87)	21 (81)	17 (85)
SY	10 (48)	3 (18)	5 (17)	5 (23)	5 (36)	2 (13)	5 (19)	3 (15)

years, 76 were defended by ASYs (83%), 14 by SYs (15%), and two by individuals of unknown age (2%). These latter two males were excluded from all analyses (Fig. 1).

The 4-year average (± SE) territory size of ASYs (1.07 ± 0.75 ha) did not differ from SYs (1.3 ± 0.23 ha; Wilcoxon signed-rank test: $Z = -1.19$, $P = 0.23$) for the territories for which we had a complete set of six 30-min observation periods on known-aged birds ($n = 90$, Table 1). Similarly, the average ASY core area for the 4 years (0.19 ± 0.14 ha) did not differ from that of SYs (0.23 ± 0.19 ha; Wilcoxon signed-rank test: $Z = -0.89$, $P = 0.37$).

The study area had a clear preponderance of older males (Table 2). A total of 108 male territories had ≥30 location observations. Of these 108 males, 91 were ASYs (84%) and 17 were SYs (16%). There were 16 additional territories mapped for which a complete set of six 30-min observation periods was not obtained, and 19 birds that were caught or mapped on the two sites, but not observed again. Of this comprehensive total of 127 birds, 27 were SYs (21.2%). Including these additional captured birds, the proportion of SYs at the red maple swamp site was 15.5% compared to 30% at the early-mid succession site. Age ratios in 2005 and 2006, the years with adequate sample sizes for comparisons, did not differ for all males considered territorial (≥30 location observations, Fisher's exact test: $P = 0.215$ in 2005, and $P = 1.00$ in 2006, Table 2).

Reproductive Success.—ASYs paired (96%, 73 of 76) at higher rates than SYs (64%, 9 of 14, $\chi^2 = 14.73$, df = 1, $P < 0.001$; Table 3) for all 4 years. However, the proportion of successfully paired males that fledged at least one young did not differ between the two age classes (ASYs = 76.7% [56 of 73], SYs = 67% [6 of 9], $\chi^2 = 0.438$, df = 1, $P > 0.05$).

Habitat Characteristics.—Twenty-one habitat characteristics were measured. One of the 21 variables was significantly different between the two age classes when combining both plots and adjusting for multiple comparisons. ASY territories had a significantly lower canopy height than those of SY birds (Wilcoxon signed-rank test: $Z = -2.13$, $P = 0.033$, Table 4). Three habitat characteristics were significantly different between age classes within each plot. On the upper plot, ASYs had significantly more song perch trees per 0.04 ha (average ± SD for ASYs = 1.98 ± 0.12 vs. 1.41 ± 0.16 for SYs, Wilcoxon signed-rank test: $Z = -2.26$, $P = 0.024$). The total number of shrub stems per 0.00785 ha (5-m radius) was significantly greater on ASY territories (average for ASYs = 42.05 ± 3.41 vs. 26.66 ± 4.05 for SYs, Wilcoxon signed-rank test: $Z = -2.61$, $P = 0.009$). On the lower plot, SYs had significantly more deciduous shrub stems >2.5 cm dbh (5-m radius) than ASYs (average for ASYs = 2.29 ± 0.32 vs. 10.13 ± 3.40 for SYs, Wilcoxon signed-rank test: $Z = -3.12$, $P = 0.002$).

DISCUSSION

The high proportion of older males in our study area, together with the high overall pairing and fledging success of males over the 4 years for all males combined clearly indicates this is a productive area for the Canada Warbler. ASY males paired at significantly higher rates than SYs, which is consistent with other warbler species, such as the Black-throated Blue Warbler (Holmes et al. 1996) and Ovenbird (Bayne and Hobson 2001). We found that ASY males were more reliably observed throughout the breeding season and a greater proportion were presumed to be territorial based upon observations of males for which we did not have sufficient data to do adaptive kernel analysis. Proportionally fewer SYs per-

TABLE 3. Number (%) of older and younger male Canada Warblers successfully pairing and fledging at least one young in each year at two sites in west-central New Hampshire during 2003 to 2006.

Age	2003		2004[a]		2005		2006	
	Paired	Fledged	Paired	Fledged	Paired	Fledged	Paired	Fledged
ASY	9/9 (100)	7/9 (78)	11/13 (85)	8/11 (73)	35/36 (97)	28/35 (80)	18/18 (100)	13/18 (72)
SY	0/1	0/0			5/7 (71)	2/5 (40)	4/6 (67)	4/4 (100)

[a] No SYs.

sisted throughout the breeding season. However, SYs demonstrated equal success in fledging ≥1 young if they were able to maintain a territory and attract a female. Certain SYs were successful in the same years that some ASYs were not. This finding demonstrates impressive variation in individual fitness across age classes. We do not have adequate data at present to analyze whether success as an SY male influences the probability of success in subsequent years.

Differences in pairing success could occur because ASY males may secure territories in habitats that females find more attractive or the males themselves may be more attractive as they are brighter, with bolder necklaces (Rappole 1983), which may signal greater experience. Bold markings have been shown to increase reproductive success of Yellow Warblers (*Dendroica petechia*) (Yezerinac and Weatherhead 1997).

There was no significant difference in size of territories (95% ADK) or core areas (50% ADK) between ASYs and SYs with complete sets of observations. This comparison was based upon combined samples from both plots. In a separate analysis, Hallworth et al. (2008) found that males of both age classes used 50% more area in the upper second-growth plot compared to the lower red maple swamp, but neither reproductive performance nor food abundance differed between the two plots. Territory size is known to vary inversely with food supply in some species (e.g., Stenger 1958). Rodenhouse and Holmes (1992) found that food-rich habitat increases reproductive success for Black-throated Blue Warblers. Paired ASY and SY Canada Warblers did not differ in the rate of fledging at least one young in our study suggesting similar food resources existed in the territories of both age classes, but we did not measure food abundance on territories for each age class of males.

Few habitat characteristics differed between ASY and SY territories. Shrub foliage densities up to 1 m on SY territories were higher than on ASY territories, but not significantly different. Shrub foliage density within this horizon on ASY territories may influence nest site selection in that dense shrubs in the lower stratum may prevent the formation of sphagnum hummocks, a nesting substrate that was

TABLE 4. Habitat characteristics sampled on territories of both ASY and SY male Canada Warblers. All habitat values denote diameter at breast height (dbh), except values under shrub foliage density, where values denote heights. Means ± SE are shown along with *Z* and *P* values with significant differences indicated by an asterisk. Canopy height was the only significantly different vegetative feature. Bonferroni adjustments for shrub stem and foliage densities were both $P = 0.01$, and $P = 0.0083$ for tree stems.

Characteristic	ASY	SY	*Z*	*P*
Canopy height, m	7.45 ± 0.26	8.91 ± 0.56	−2.130	0.033*
Song posts, 0.04 ha	1.92 ± 0.10	2.06 ± 0.25	−0.555	0.579
Sum shrubs	45.20 ± 2.02	44.55 ± 3.10	−0.151	0.880
Deciduous shrubs, >1 m				
<2.5 cm	30.46 ± 2.98	22.17 ± 3.58	−0.331	0.741
>2.5 cm	6.20 ± 0.96	5.39 ± 1.48	−0.238	0.815
Coniferous shrubs, >1 m				
<2.5 cm	10.40 ± 1.09	8.03 ± 1.12	−0.506	0.613
>2.5 cm	4.19 ± 0.33	4.00 ± 0.61	−0.302	0.763
Shrub foliage density				
0–0.5 m	0.88 ± 0.20	1.87 ± 0.48	−2.269	0.023
0.5–1 m	1.13 ± 0.29	1.73 ± 0.50	−2.057	0.040
1–1.5 m	1.10 ± 0.21	1.49 ± 0.33	−1.793	0.073
1.5–2 m	0.91 ± 0.13	1.45 ± 0.28	−1.793	0.073
2–2.5 m	0.94 ± 0.16	1.71 ± 0.42	−1.698	0.090
Trees				
Small, 8–22.9 cm	13.30 ± 0.82	16.43 ± 2.08	−1.515	0.130
Medium, 23–37.9 cm	2.34 ± 0.34	2.64 ± 0.55	−0.813	0.416
Coniferous trees				
Small, 8–22.9 cm	6.69 ± 0.62	7.33 ± 1.28	−0.597	0.550
Medium, 23–37.9 cm	0.90 ± 0.14	1.08 ± 0.25	−1.165	0.244
Deciduous trees				
Small, 8–22.9 cm	6.51 ± 0.57	9.05 ± 1.24	−1.916	0.055
Medium, 23–37.9 cm	1.32 ± 0.16	1.56 ± 0.51	−0.80	0.936
Snags				
Sum of all size classes	1.75 ± 0.22	2.69 ± 0.86	−0.929	0.353
Small, 8–22.9 cm	1.59 ± 0.22	2.48 ± 0.85	−0.831	0.406
Medium, 23–37.9 cm	0.16 ± 0.04	0.20 ± 0.09	−0.845	0.398

common if not preferred (Conway 1999, this study). Twelve of 18 nests found in 2005 and 2006 were within sphagnum hummocks, and were among the most cryptic of nest locations. In contrast, greater shrub cover on SY territories may inhibit the ability of predators from locating nests (Bowman and Harris 1980).

Average canopy height was significantly lower within ASY territories compared to SY territories. The lower canopy height on ASY territories for both plots may factor into female assessment of prospective mates. We found that ASYs had more song perch trees and total shrub stem densities on the upper, second-growth plot in the single-plot habitat analyses between age classes. The greater number of emergent perch sites and higher total shrub stem densities in this second-growth may combine to attract females more frequently to ASY territories, which is consistent with the higher pairing success of ASYs in our study. Larger shrubs (>2.5 cm dbh) were more abundant on SY territories on the lower, red maple swamp plot. ASYs occupied most of the dense deciduous thickets typical of red maple swamp on the lower plot. These dense thickets tended to have stems <2.5 cm dbh, whereas peripheral areas had larger-stemmed shrubs. The latter was more typical of SY territories on the lower plot.

The habitat complex in which this study was conducted is presumed to be of high qual-

ity given the high ASY: SY ratio (Hunt 1996) and reproductive success (Holmes et al. 1996) of territory-holders. More work needs to be done to compare ASY and SY reproductive performance in areas with different demographic ratios assuming that within-population differences are likely to be more pronounced in more marginal habitat.

ACKNOWLEDGMENTS

This research was supported by the New England Institute for Landscape Ecology, Plymouth State University, the Vermont Institute of Natural Science, Sweet Water Trust, The A. V. Stout Fund, and the Charles E. and Edna T. Brundage Scientific and Wildlife Conservation Foundation. We thank Jameson Chace for introducing us to key methods used in this study. Clinton Parrish, Robin Jahne, Amy Ueland, Eric Anderson, Nicholas Dalzell, Keith Doran, Christopher Bordonaro, Marissa Goodnow, and Kyle Parent assisted in data collection. J. A. Jones and C. E. Braun made valuable comments on the manuscript. We thank the Town of Canaan and the Mascoma Watershed Conservation Council for permission to use the study sites.

LITERATURE CITED

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

Bayne, E. M. and K. A. Hobson. 2001. Effects of habitat fragmentation on pairing success of Ovenbirds: importance of male age and floater behavior. Auk 118:380–388.

Bowman, G. B. and L. D. Harris. 1980. Effect of spatial heterogeneity on ground-nest depredation. Journal of Wildlife Management 44:806–813.

Conway, C. J. 1999. Canada Warbler (*Wilsonia canadensis*). The birds of North America. Number 421.

DeGraaf, R. M., J. B. Hestbeck, and M. Yamasaki. 1998. Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine. Forest Ecology and Management 103:217–233.

Ficken, M. and R. W. Ficken. 1966. Notes on mate and habitat selection in the Yellow Warbler. Wilson Bulletin 78:232–233.

Golet, F. C., Y. Wang, J. S. Merrow, and W. R. DeRagon. 2001. Relationships between habitat and landscape features and the avian community of red maple swamps in southern Rhode Island. Wilson Bulletin 113:217–227.

Hagan, J. M., P. S. McKinley, A. L. Meehan, and S. L. Grove. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. Journal of Wildlife Management 61:718–735.

Hallworth, M. T., P. M. Benham, J. D. Lambert, and L. R. Reitsma. 2008. Canada Warbler (*Wilsonia canadensis*) breeding ecology in young forest stands compared to a red maple (*Acer rubrum*) swamp. Forest Ecology and Management 255: 1353–1358.

Harvey, P. H., M. J. Stenning, and B. Campbell. 1985. Individual variation in seasonal breeding success of Pied Flycatchers (*Ficedula hypoleuca*). Journal of Animal Ecology 54:391–398.

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. Journal of Animal Ecology 65:183–195.

Howlett, J. S. and B. J. M. Stutchbury. 2003. Determinants of between-season site, territory, and mate fidelity in Hooded Warblers (*Wilsonia citrina*). Auk 120:457–465.

Hunt, P. D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwoods forest: evaluation of habitat quality. Auk 113:875–888.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1994. CALHOME Home range analysis program. USDA, Forest Service, Pacific Southwest Research Station, Fresno, California, USA.

Martin, T. E. and C. J. Conway. 1994. Breeding Bird (BBIRD) field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.

Nol, E. and J. N. M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. Journal of Animal Ecology 56:301–313.

Perrins, C. M. and R. H. McCleery. 1985. The effect of age and pair bond on the breeding success of Great Tits *Parus major*. Ibis 127:306–315.

Pyle, P. 1997. Identification guide to North American birds. Part I. Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, USA.

Rappole, J. H. 1983. Analysis of plumage variation in the Canada Warbler. Journal of Field Ornithology 54:152–159.

Rodenhouse, N. L. and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. Ecology 73:357–372.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, results and analysis 1966–2004. Version 2005.2. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.usgs.gov/bbs/bbs.html (accessed 12 October 2006).

Sherry, T. W. and R. T. Holmes. 1989. Age-specific social dominance affects habitat use by breeding American Redstarts (*Setophaga ruticilla*): a removal experiment. Behavioral Ecology and Sociobiology 25:327–333.

Stenger, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk 75: 335–346.

TITTERINGTON, R. W., H. S. CRAWFORD, AND B. N. BURGASON. 1979. Songbird response to commercial clear-cutting in Maine spruce-fir forests. Journal of Wildlife Management 43:602–609.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

VICKERY, P. D., M. L. HUNTER, AND J. V. WELLS. 1992. Is density an indicator of breeding success? Auk 109:706–710.

YEZERINAC, S. M. AND P. J. WEATHERHEAD. 1997. Extra-pair mating, male plumage coloration and sexual selection in Yellow Warblers (*Dendroica petechia*). Proceedings of the Royal Society of London Series B 264:527–532.

ZANETTE, L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. Journal of Avian Biology 32: 38–46.

The Wilson Journal of Ornithology 120(3):455–459, 2008

SOLITARY WINTER ROOSTING OF OVENBIRDS IN CORE FORAGING AREA

DAVID R. BROWN[1,2,3] AND THOMAS W. SHERRY[1]

ABSTRACT.—We used radio-telemetry to locate night roosts of 54 Ovenbirds (*Seiurus aurocapilla*) wintering in a coastal second-growth scrub habitat in Jamaica. All Ovenbirds roosted within their daytime home range and most individuals roosted within the core of their diurnal home range. Sixty-six percent of individuals roosted within the 30% core use distribution (i.e., most heavily used portion of their home range) and 35% of individuals roosted within the 10% core. The average distance between roost sites for 29 individuals located on more than one night was 34 m and at least three birds roosted solitarily in the same location on different nights. Roost location relative to the 10% core area of diurnal home range did not differ between males and females, adults and immatures, or between individuals studied in subsequent years. The wintering Ovenbird population we studied appeared to roost solitarily. This study is the first to provide quantitative evidence that individual migrant songbirds in a tropical wintering population consistently roost at night within their foraging home range. These results suggest that roosting behavior is correlated with daytime space use patterns of the winter social system. *Received 29 May 2007. Accepted 7 January 2008.*

Our knowledge of roosting behavior of tropical wintering migrant songbirds is limited. The only quantitative studies of winter roosting are for species that roost in separate habitats from their daytime activity: Prothonotary Warbler (*Protonotaria citrea*) (Warkentin and Morton 1995), and Northern Waterthrush (*Seiurus noveboracensis*) (Reitsma et al. 2002, Burson et al. 2005). The literature is limited to descriptive examples of communal roosting of Northern Parula (*Parula americana*) (Staicer 1992), Cape May Warbler (*Dendroica tigrina*) (Staicer 1992, Baltz and Latta 1998), Prairie Warbler (*D. discolor*) (Staicer 1992), and Prothonotary Warbler. Morton (1980) and Staicer (1992) observed individuals going to roost and vocalizing at dawn on diurnal home ranges, and it is generally assumed that many winter-territorial migrant songbirds roost solitarily at night on their diurnal home range. However, quantitative evidence of these patterns is lacking. Roosting behaviors have conservation implications because multiple habitats may require protection for species that roost in habitats separate from their diurnal activities.

We describe (1) the roosting behavior of wintering Ovenbirds (*Seiurus aurocapilla*) in Jamaica based on radio-tracking data, and (2) consider how roosting behavior is associated with other aspects of the winter social system. Specifically, we predicted that Ovenbirds would roost solitarily within their home range because most wintering Ovenbirds maintain long-term, minimally overlapping home range cores.

METHODS

We located roosts of Ovenbirds in a second growth scrub habitat at Luana Point, 8 km west of Black River, Jamaica (18° 02′ N, 77° 55′ W) during the dry season of February and March 2003–2005. The scrub habitat is relatively homogeneous and dominated by Logwood (*Haematoxylum campechianum*), a dry deciduous introduced tree that ranged in height from 3 to 8 m (Strong 2000). The study area includes patches of black mangrove (*Avicennia germinans*) and red mangrove (*Rhizophora mangle*) within 50–200 m of scrub study plots. Ovenbirds were abundant within the scrub habitat leaving little, if any, unoccupied space (Brown 2006). We mist-netted individuals, and banded and classified them to age (adult or immature). We ascertained gender using molecular markers or morphological measurements (Brown and Sherry 2006). Radios weighing 0.6–0.9 g (Holohil Systems Ltd., Carp, ON, Canada) were attached with leg-loop harnesses (Rappole and Tipton 1991). We began searching for roosts 1 hr past

[1] Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118, USA.

[2] Current address: Department of Biological Sciences, Eastern Kentucky University, Richmond, KY 40475, USA.

[3] Corresponding author; e-mail: david.brown5@eku.edu

sunset. Roosts were located either by direct searches until we isolated the site or by triangulation with Program LOAS (Ecological Software Solutions 2002). We also collected locations ($\bar{x}$ = 39, SE = 1) of each bird during the day, and modeled home range characteristics using fixed-kernel use distributions with Arcview 3.2 (Hooge and Eichenlaub 1997). A use distribution is a probability density function of the frequency of use of a given area within the home range based on the density of all locations (Kernohan et al. 2001). We report the area contained within a fixed category (e.g., 10%, 30%, 95%) of the use distribution volume. Smoothing parameters for fixed-kernel functions were selected by least squares cross validation.

We calculated average home range size and neighbor overlap for 95% and 30% use distributions. We considered the 30% use distribution to be the core area but, for some analyses, used the 10% core area to delineate the center of activity more precisely. We identified where birds roosted in relation to their home ranges using the distance from the roost site to the edge of the 10% core area, (distance = zero for roosts within this core). We also classified which kernel contour, in increments of 10%, contained each roost location and used a histogram to compare this graphically to the total home range area within each 10% increment.

We had only a single roost location for many birds. We considered individual birds rather than roost sites as replicates by randomly selecting one location for analyses of roost proximity to home range core for the subset of individuals for which we had multiple locations. We examined if birds tended to roost close to their home range core using a paired *t*-test that compared distances to home range cores from actual roost sites versus the average distance of 10 random locations within each home range. Random locations were selected uniformly across the home range and not with respect to areas of increased use. We arbitrarily selected 10 as the sample size of random locations because we believed it would produce an adequate average distance. We tested for differences between males and females, and ages in the distance of roosts from home range cores using a two-way ANOVA. Test assumptions were not violated and no data transformations were conducted. We used Systat Version 10 (Wilkinson 2000) for all analyses and report means ± SE.

RESULTS

Mean (± SE) home range area of 90 sedentary (non-floating) birds was 0.69 ± 0.05 ha (area of 95% fixed-kernel use distribution). Mean 30% use distribution core area was 0.04 ± 0.004 ha. Neighboring home ranges overlapped considerably (overlap area of 95% use distribution with each neighbor = 22%), but core areas overlapped little (overlapping area of 30% core with each neighbor = 3%).

We located at least one night roost of 54 individuals and multiple roost locations for 29 of these birds. No roost was outside the home range (Fig. 1), but most birds (n = 26) roosted in different locations when tracked on multiple nights (average distance from previous roost site = 34 ± 4 m). The other three Ovenbirds roosted close to the previous sites, i.e., within the same tree. Roost locations were closer than random locations to home range cores (t_{54} = 9.34, $P < 0.001$). The distance from the 10% contour of the home range to actual roosts was 7 ± 1 m compared with 36 ± 3 m at random locations. The distance of roost locations from home range cores did not differ by gender ($F_{1,48}$ = 2.04, P = 0.16; n = 25 males, 25 females), age class ($F_{1,52}$ = 0.14, P = 0.71; n = 30 adults; n = 24 immatures), or year ($F_{2,51}$ = 1.13, P = 0.33; 2003: n = 10, 2004: n = 24, 2005: n = 20). Sixty-six percent of roosts were within the 30% core area of the use distribution, which encompassed only 7% of the total area of the home range (Fig. 2). Territorial birds, regardless of age or gender roosted centrally in relation to where they foraged. Birds were at least 2 m above ground for several cases (n = 7) where we identified the roost tree.

DISCUSSION

Ovenbirds roosted exclusively within their home range and most individuals roosted within their home range core. We did not directly observe solitary roosting (i.e., it is possible that more than one individual roosted in close proximity), but our results support solitary roosting because Ovenbird home range cores overlapped minimally. Thus, roost locations also must have been separated. This is

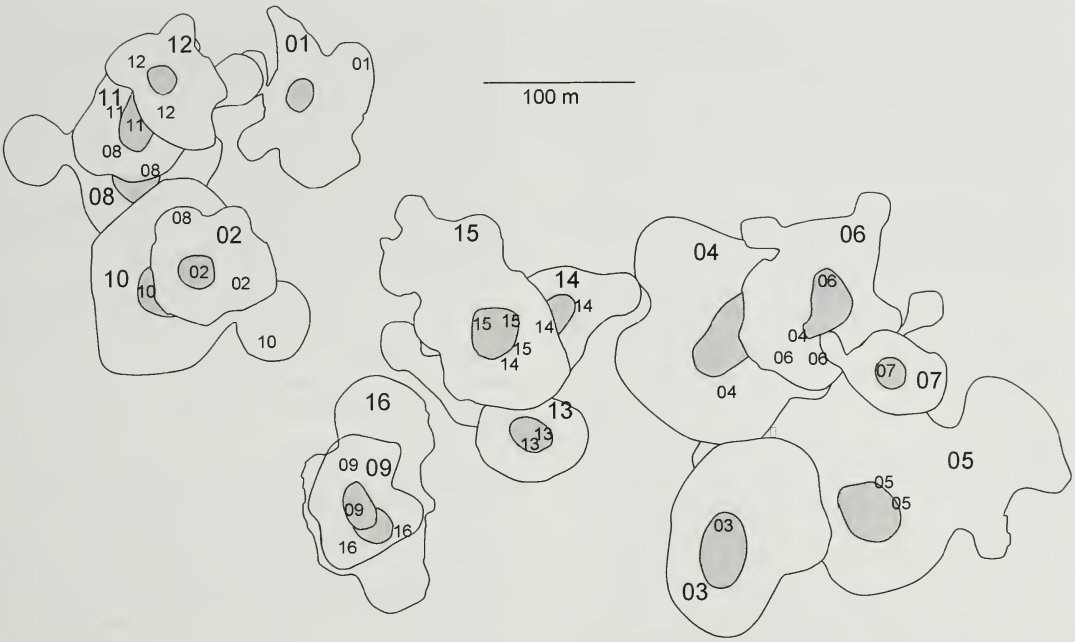


FIG. 1. Home ranges of 16 Ovenbirds (individuals labeled with large numbers) radio-tracked in a single winter season (2005) relative to night roost locations (small numbers). Home range contours were derived from 30% (shaded areas) and 95% (outline) fixed-kernel use distributions. Individuals located on multiple nights are indicated by multiple small numbers. Numerous non radio-marked Ovenbirds were also in the study area.

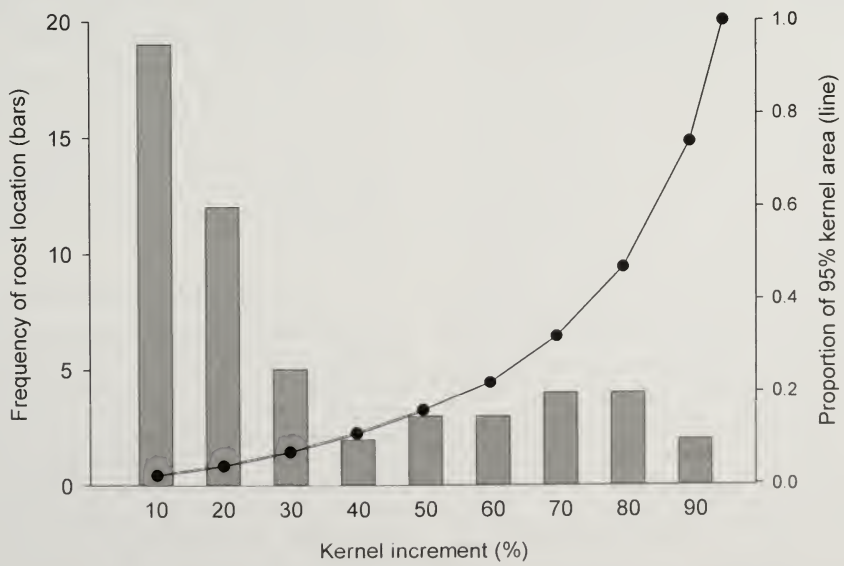


FIG. 2. Frequency of roost locations of Ovenbirds by kernel increment. Bars indicate the number of individuals located once each at night roost sites for fixed percentages of each bird's use distribution. Core areas (10–30%) contain a small proportion of the total home range area (line). Each category represents the percentage of the total volume of the use distribution, but may represent a smaller proportion of the home range area. For example, the 50% use distribution encompasses 50% of a bird's activity, but only 16% of the total home range area.

the first quantitative description of a neotropical migrant songbird roosting solitarily within the core of its foraging home range. We cannot rule out the possibility that Ovenbirds roost communally or outside their home range elsewhere, but the social behavior at our Jamaican study site is typical of that in other habitats (Strong and Sherry 2000); we suspect the roosting pattern is typical as well.

Few comparable data are available for other migratory species. Radio-tracked Hermit Thrushes (*Catharus guttatus*) wintering in the temperate zone also roosted solitarily within their diurnal home range (Brown et al. 2000). Many species of migratory songbirds occupy small home ranges in winter and it is likely that some of these also roost within their home range. Evidence of large-scale movements for most species at dusk is lacking and Morton's (1980) observations are supportive. However, other patterns of roosting have also been documented. Wintering Bicknell's Thrushes (*C. bicknelli*), which occupy exclusive territories during the day, were radio-tracked to "loosely communal" night roosts in a separate forest habitat from their diurnal activities, presumably because of predation threat from rats (*Rattus* spp.) in their preferred habitat (Rimmer et al. 2001:13). At least some individuals of Cape May Warbler, Prairie Warbler, and Northern Parula roosted communally, and most individuals of these species generally maintain solitary home ranges (Staicer 1992). Diurnal space use or roosting patterns for these three species has not been measured with telemetry, which is the best technique to quantify secretive space use patterns. Individual Northern Waterthrush forage solitarily, shifting habitat use to track seasonal changes in food supply, and roost in structurally complex stands of red mangrove some distance from foraging locations (Reitsma et al. 2002, Burson et al. 2005). Wintering Prothonotary Warblers forage in mono- and interspecific flocks, and roost communally in mangrove habitat (Petit 1999). Movement to red mangrove roost sites by both Northern Waterthrush and Prothonotary Warblers may be an anti-predation behavior, because these mangrove stands are isolated from dry land. However, movement to a distinctive roosting habitat also corresponds with the absence of stable, long-term (over winter) home ranges. We hypothesize, based on these patterns, that winter roost behavior is associated with diurnal social systems, as exemplified by both solitary foraging and roosting by Ovenbirds. However, considerable variation in social behavior exists both within and among species of wintering neotropical migrants, and additional research is needed to advance understanding of the causation of roosting behavior.

We do not understand why Ovenbirds tended to roost near their core diurnal foraging area and not randomly in their winter home range or in separate habitats. The relatively sedentary behavior of Ovenbirds would tend to minimize energetic costs associated with commuting. It is unlikely these costs would be important considering the small size of Ovenbird home ranges and the proximity of our study site to red mangrove habitat (<50 m for some birds). Roosting behavior of tropical wintering birds is likely not subject to thermoregulatory constraints. We suggest it is more likely that roosting behavior is associated with social system or other ecological factors including predation. Roosting within core foraging areas would tend to space individuals throughout the habitat, which could help protect against particular predators.

Roosting behavior is important beyond our understanding of habitat use and social systems. Conservation planning necessitates integrating day with night activity locations for several species that roost apart from where they forage. Conservation planning is considerably simplified for species that roost within their daytime home range, as do these Ovenbirds.

ACKNOWLEDGMENTS

We are indebted to field assistants Adam Anderson, Lynn Duda, Andrea Flowers, Lucas Forester, and Greg Levandoski. S. L. Burson and 2 anonymous reviewers provided constructive comments on the manuscript. Bird banding and radio-marking were conducted with approval of the U.S. Geological Survey and the Jamaican National Environment and Planning Agency. This work was funded by a National Science Foundation (NSF) grant to TWS (DEB-0089541) and an NSF Doctoral Dissertation Improvement Grant to DRB and TWS (DEB-0408117).

LITERATURE CITED

Baltz, M. E. and S. C. Latta. 1998. Cape May Warbler (*Dendroica tigrina*). The birds of North America. Number 332.

Brown, D. R. 2006. Food supply and the dry-season ecology of a tropical resident bird community and an over-wintering migrant bird species. Dissertation. Tulane University, New Orleans, Louisiana, USA.

Brown, D. R. and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22–32.

Brown, D. R., P. C. Stouffer, and C. M. Strong. 2000. Movement and territoriality of wintering Hermit Thrushes in southeastern Louisiana. Wilson Bulletin 112:347–353.

Burson, S. L., L. R. Reitsma, and P. D. Hunt. 2005. Conservation implications of multiple habitat use by Northern Waterthrushes during the nonbreeding season. Journal of Caribbean Ornithology 18: 72–76.

Ecological Software Solutions. 2002. LOAS. Ecological Software Solutions LLC, Schwagalpstrasse 2, 9107, Urnasch, Switzerland.

Hooge, P. and B. Eichenlaub. 1997. Animal movement extension 2.0. Alaska Science Center, Biological Science Office, USDI, Geological Survey, Anchorage, Alaska, USA.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 126–166 *in* Radio tracking and animal populations (J. J. Millspaugh and J. M. Marzluff, Editors). Academic Press, San Diego, California, USA.

Morton, E. S. 1980. Adaptations to seasonal changes by migrant land birds in the Panama Canal Zone. Pages 437–453 *in* Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, Editors). Smithsonian Press, Washington, D.C., USA.

Petit, L. J. 1999. Prothonotary Warbler (*Protonotaria citrea*). The birds of North America. Number 408.

Rappole, J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62: 335–337.

Reitsma, L., P. Hunt, S. L. Burson, and B. B. Steele. 2002. Site fidelity and ephemeral habitat occupancy: Northern Waterthrush use of Puerto Rican black mangroves during the nonbreeding season. Wilson Bulletin 114:99–105.

Rimmer, C. C., K. P. McFarland, W. G. Ellison, and J. E. Goetz. 2001. Bicknell's Thrush (*Catharus bicknelli*). The birds of North America. Number 592.

Staicer, C. A. 1992. Social behavior of the Northern Parula, Cape May Warbler, and Prairie Warbler wintering in second-growth forest in southwestern Puerto Rico. Pages 308–320 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Editors). Smithsonian Institution Press, Washington, D.C., USA.

Strong, A. M. 2000. Divergent foraging strategies of two neotropical migrant warblers: implications for winter habitat use. Auk 117:381–392.

Strong, A. M. and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of Ovenbirds wintering in Jamaica. Journal of Animal Ecology 69:883–895.

Warkentin, I. G. and E. S. Morton. 1995. Roosting behavior of Prothonotary Warblers in the nonbreeding season. Wilson Bulletin 107:374–376.

Wilkinson, L. 2000. Systat 10.0 for Windows. SPSS Inc., Chicago, Illinois, USA.

The Wilson Journal of Ornithology 120(3):460–466, 2008

REPRODUCTIVE SUCCESS OF THE PUERTO RICAN VIREO IN A MONTANE HABITAT

ADRIANNE G. TOSSAS[1,2]

ABSTRACT.—I studied the reproductive success of the Puerto Rican Vireo (*Vireo latimeri*) from 1998 to 2000 in Maricao State Forest, a montane reserve in the southwestern part of Puerto Rico. No parasitism by the Shiny Cowbird (*Molothrus bonariensis*) was found but 63% of 38 active nests were depredated with an overall daily nest survival of 0.932 ± 0.007 (± SE). Mean nest survival estimates following Hurricane Georges did not vary significantly before and after the hurricane. However, a return rate of only 39% was estimated for color-marked adults the year including the hurricane compared to 72% for the year without a hurricane. A 26% decline in density of territorial males was observed in the post-hurricane year. *Received 26 May 2007. Accepted 11 November 2007.*

The nesting success of a bird species can vary geographically as a result of differences in abundance of brood parasites, particularly if habitat characteristics favor the parasitic species (Ward and Smith 2000, Purcell 2006). These effects can be exacerbated if the host has not evolved nest defense strategies following recent colonization by the parasitic species (Rothstein 1990). This may be the case of the Puerto Rican Vireo (PRVI; *Vireo latimeri*), which has experienced sharp decreases in population size in Guánica State Forest (henceforth Guánica) on the dry coastal plain in southern Puerto Rico (Faaborg et al. 1997). However, the species is still commonly found throughout the island (Raffaele 1989). The population decline has been mainly associated with high rates (73–83%; Woodworth 1997) of brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*), a species first reported in Guánica by 1969 (Kepler and Kepler 1970), while expanding its range into the Caribbean region from its native distribution in South America (Cruz et al. 1985). The PRVI population in Guánica from 1973 to 1996 showed an average annual decrease of 5% (Faaborg et al. 1997). Mean annual survival estimates for the PRVI in Guánica decreased from 0.68 in 1973–1990 (Faaborg and Arendt 1995) to 0.61 for a longer time period including data through 1996 (Faaborg et al. 1997).

Little is known about the reproductive success of the PRVI and the effects of cowbird parasitism in habitats other than Guánica. Parasitism rates may differ within the island, particularly since the Shiny Cowbird is rare or absent in some habitats. Cowbird parasitism of vireo nests has been found to be less intensive in highly forested montane habitats than in the more fragmented coastal habitats (Cruz et al. 1985, Pérez-Rivera 1986). Pérez-Rivera (1986) reported that 36% of PRVI nests and 35% of Black-whiskered Vireo (*Vireo altiloquus*) nests in the central mountain region were parasitized. In contrast, cowbirds parasitized 87% of the Black-whiskered Vireo nests in coastal forests (Cruz et al. 1985).

The objectives of my study were to examine if the Puerto Rican Vireo was affected by Shiny Cowbird parasitism in Maricao as has been reported in Guánica (Woodworth 1997, 1999; Woodworth et al. 1998, 1999), and to compare the breeding biology between the two populations. The incidental passage of Hurricane Georges through the Maricao study area in September 1998 provided an opportunity to evaluate how reproductive parameters were affected by the natural event. I hypothesized that higher nesting success should occur at Maricao due to the scarcity of cowbirds at this site, compared to Guánica, and that parameters related to the breeding biology of the Puerto Rican Vireo should differ in the years before and after the passage of the hurricane.

METHODS

Study Area.—Maricao (18° 09′ N, 66° 59′ W) is in the western part of the central mountain range of Puerto Rico, 16 km northwest of

[1] Department of Biology, University of Puerto Rico, Río Piedras, Puerto Rico 00931, USA.

[2] Current address: Villas del Río, 1100 Bambú, Mayagüez, Puerto Rico 00681, USA;
e-mail: agtossas@gmail.com

Guánica. It comprises 4,150 ha with elevations ranging from 150 to 875 m (Silander et al. 1986). Annual rainfall and temperature from 1961 to 1990 averaged 232.6 cm and 21.7° C, respectively. The area contains subtropical moist forest, subtropical wet forest, and lower montane wet forest (Ewel and Whitmore 1973). Dominant tree species include *Micropholis chrysophylloides*, *Terebraria resinosa*, *Linociera dominguensis*, *Homalium racemosum*, *Tabebuia schumanniana*, and *Eugenia stahlii* (Silander et al. 1986).

Maricao was struck by Hurricane Georges on 21–22 September 1998. This hurricane (category 3 on Saffir-Simpson scale of 5) damaged the forest structure with sustained winds of 184 kph and gusts of 240 kph (Bennett and Mojica 1998). The strong winds opened the canopy by severe defoliation, tree falls, and stem and branch breakage, all of which affected the resident avifauna (Tossas 2006).

Nest Searching and Monitoring.—Thirty-six adult PRVIs were color-banded from 1998 to 2000 to facilitate behavioral observations. Individuals were lured to mist nets by playing the male's song on a tape recorder near or within their territories. Gender, age, and breeding condition were assigned for captured vireos when possible. Twenty adult vireos were confidently separated by gender, 15 were males and five were females. All captured individuals were marked with a USGS aluminum band and a unique combination of two plastic color bands. At least one member of all pairs studied was color-banded.

Vireo pairs were monitored from March to July each year from 1998 to 2000 along three trails with similar floristic composition and vegetation structure. I followed singing males looking for behavioral cues that could lead to their nests, or pairs carrying nesting material up to ~50 m into the forest on each side of the trails surveyed. Nest contents were examined every 2–5 days for signs of predation, parasitism or nest abandonment. Nests were checked directly or with a mirror fixed to a 6-m pole. Nests were checked when possible from a distance of ~10 m to avoid disturbing breeding pairs, altering the nesting habitat, or increasing the risk of predation. I looked for Shiny Cowbird eggs or chicks in PRVI nests as signs of brood parasitism. Predation was assumed if eggs disappeared before their hatching date. Chicks were considered predated if they disappeared from the area around the nest before the expected fledging date. Incubation and nestling stages are 15 and 12 days, respectively (Woodworth 1997). The dates marking the initiation or end of each stage were assigned by direct observation or by back-dating or forward-dating from other observed events. Nest abandonment was recorded if adults or chicks were not seen in the nest or in the vicinity during three consecutive visits of 30 min each. I noted if abandoned nests included eggs or were empty.

Nest searching in 1999 was limited because of changes in forest structure related to Hurricane Georges and management practices that restricted access to trails. However, I monitored pairs throughout the breeding season and was able to ascertain their productivity even when I did not find the nest structures. Breeding season length was calculated for each study year from the day when the first pair started building a new nest until no active nests were found.

Nest Success.—Daily nest survival rates and standard errors were generated following Mayfield (1975) and Johnson (1979). Estimates were calculated for two nesting intervals separately, from egg laying to incubation, and for the nestling period. An overall estimate was calculated for both intervals combined.

Index of Annual Reproductive Success.—An estimate of annual reproductive success was calculated for all nests built by a pair monitored throughout the entire breeding season. However, only single nests were found for most pairs in 1998 (17/22) and 2000 (11/22), and only three nests were monitored in 1999. Thus, identifying whether a pair had successfully raised chicks was based on observations of juveniles attended by color-marked adults at the end of the breeding season. This method was possible because juvenile PRVIs remain within their natal territories and are fed by adults for as long as 2 months after fledging (pers. obs.).

Territories of color-marked individuals were visited every 2–5 days throughout the breeding season in search of nests, but searches for juveniles were more intensive from June to

July, the final weeks of the breeding season. I played the song of the PRVI in a tape recorder 1–2 times from the center of each territory for 5-min intervals and looked for both members of the pair during visits that lasted from 30 min to 1 hr. Adults usually approached the source of the intruder's song and responded with alarm calls, providing an opportunity to observe accompanying juveniles. Each territory was visited 10–15 times, and 20–22 pairs were monitored each year with at least one member of the pair being observed in every visit.

I calculated the proportion of juveniles attended by adults as an index of annual reproductive success by the end of the breeding season. The index was the mean number of young fledged/pair/year. This method may underestimate reproductive success if chicks were depredated after leaving the nest, if their presence was not detected by being concealed and quiet, or if the brood was split between the pair. However, even with these biases, the index allows comparisons among study years.

Shiny Cowbird Surveys.—I performed 60 point counts with playbacks of the Shiny Cowbird chatter call along the two trails where I did most nest searching. Counts were conducted in June 1998 (n = 30) and 1999 (n = 30) when PRVIs and most resident bird species were breeding. Fifteen point counts of unlimited radius, 100 m apart, were conducted in each trail. I played the call in the center of each plot for 5 min and waited 5 min for a cowbird aural or visual response. I also carefully looked for indications of cowbird presence during field visits throughout the project.

Return Rates and Territory Mapping.—Marked PRVIs were followed over time to obtain estimates of their return rates (finite survival rate described by Krebs 1989). The annual return rate was estimated as the number of marked adults present in their territories in year t that were recaptured or reobserved in their territories in year t + 1. The probability of relocating banded PRVIs using this method is high (Woodworth et al. 1999), although it does not account for individuals that may be alive but not in the sampling area. Thus, adults were assumed to have died or dispersed outside the search area if not observed the following year. The study included 26 adult vireos color-banded in 1998 (n = 13) and 1999 (n = 13). Males and females were pooled for analysis due to small sample size and inability to differentiate gender of all individuals. Return rates were calculated for two time periods, a year including the hurricane event (1998–1999) and a year without a hurricane (1999–2000). Confidence intervals for return rates were calculated assuming binomial sampling.

Spot maps were prepared for PRVIs along three transects to measure size and density of male territories. I assumed territorial boundaries occurred where males or pairs engaged in aggressive encounters with neighbors and intruders (Bibby et al. 2000). The location of singing males, nests, and movements of individuals also helped delineate territories. The mating status of males was assigned from observations during repeated visits to the territories throughout the breeding season. Unpaired males were excluded from the total density of territorial males (Wenny et al. 1993). All results are presented as mean (± SD), except for nest survival rates ($\bar{x}$ ± SE).

RESULTS

Nest Success.—I found 38 active PRVI nests in Maricao during the breeding seasons of 1998 to 2000. Most were found during nest building or early in the incubation period. All cases of nesting failure (24 of 38 nests) were attributed to predation, resulting in loss of the entire clutch or brood. Average clutch size was 2.03 ± 0.16 eggs (range = 2–3, n = 38). Mean nest height was 4.9 ± 1.29 m (range = 2.4–7.0 m, n = 19). Breeding seasons lasted 90, 107, and 88 days in 1998 (26 Apr to 24 Jul), 1999 (23 Mar to 15 Jul), and 2000 (14 Apr to 10 Jul), respectively. Nesting activity was not observed after 15 July of any year.

None of the PRVI nests was parasitized by the Shiny Cowbird. Cowbirds were not detected on any of the point counts in the forest interior with or without playbacks. I only had incidental observations of individual cowbirds outside of the study sites, along edges or in disturbed areas such as around the forest headquarters and near the communications antennae and vacation center. I observed single cowbirds on two occasions following Greater Antillean Orioles (*Icterus dominicensis*) at the forest edge and twice observed single cowbirds flying high over the forest canopy.

TABLE 1. Nest survival rates ($\bar{x} \pm$ SE) of the Puerto Rican Vireo in Maricao State Forest, Puerto Rico, 1998–2000.

Year	Nests	Observation days	Daily survival rates[a]		
			Egg laying and incubation	Nestling	Overall (egg laying through nestling)
1998	20	411	0.981 ± 0.008	0.953 ± 0.017	0.935 ± 0.029
1999	2	27	[b]		
2000	16	246	0.951 ± 0.017	0.976 ± 0.017	0.928 ± 0.013
Totals	38	684	0.968 ± 0.008	0.963 ± 0.012	0.932 ± 0.007

[a] Incubation and nestling stages consist of 15 and 12 days, respectively (Woodworth 1997).
[b] Analysis not possible due to small sample size, data added to total.

Fourteen nests were lost during 440 nest-days of incubation and nine nests were lost during 244 days of the nestling stage (Table 1). The probabilities ($\bar{x} \pm$ SE) that a nest would survive 15 days of incubation and 12 days of the nestling stage were 0.62 ± 0.008 and 0.64 ± 0.012, respectively. The probability of survival from incubation to fledging was 40%. Daily survival rates did not differ between the incubation and nestling periods ($\chi^2_1 = 4.08$, $P = 0.25$) or between study years ($\chi^2_3 = 0.05$, $P = 0.83$).

Annual Reproductive Success.—Puerto Rican Vireo pairs in Maricao renested as many as three times in a single season after losses to predation, but most pairs (17/22, based on 1998 data) had a single nest. The percent of successful pairs ranged from 36 in 1998 to 65 in 1999, and was 55% in 2000. None of the pairs had two successful clutches in one season. A total of 40 fledglings was produced by 33 successful pairs ($n = 64$ total pairs) during the 3 years. Successful pairs produced an average (± SD) of 1.21 ± 0.55 fledglings/year, ranging from 1.15 ± 0.55 fledglings/pair in 1999 to 1.25 ± 0.62 fledglings/pair in 2000.

I was able to follow 16 PRVI pairs for more than one breeding season. Most pairs (81%) were successful in at least 1 of the 3 years. Four of the nine pairs I observed during 1998-2000 were successful once, two were successful twice, and three pairs failed to produce fledglings in any year. None of the pairs was successful in all 3 years. Seven pairs were followed in two breeding seasons. Three successfully reared young in both years, while the rest were successful in 1 year. Fifty-one percent of all pairs ($n = 64$ pair years) produced offspring in at least 1 year.

Return Rates and Territory Size.—The return rate ($\bar{x} \pm$ SD) of territorial adults from 1998 to 1999 was 0.39 ± 0.14 ($n = 5/13$; 95% CI = 0.14–0.68). Thirteen individuals marked in 1999 were added to the sample group of five survivors from 1998. The return rate from 1999 to 2000 was 0.72 ± 0.11 ($n = 13/18$; 95% CI = 0.47–0.90). None of the individuals marked in 1998 and missing in the 1999 sampling period was reobserved in 2000.

Mean (± SD) territory size was 0.86 ± 0.20 ha and ranged from 0.56 to 1.08 ha ($n = 9$). I did not observe territory switching in marked individuals. Ninety-one percent of all territorial males (1998–2000) were paired ($n = 69$). This number ranged from 96% in 1998 ($n = 23$) to 87% in 1999 ($n = 23$) and 91% in 2000 ($n = 23$). Density of male territories was 0.57, 0.44, and 0.41/ha, in 1998, 1999, and 2000, respectively.

DISCUSSION

The main difference in nesting success between Maricao and Guánica PRVI populations was related to parasitism rates. Brood parasitism was absent in the montane population, but 73–83% of the nests in the lowland were parasitized by the Shiny Cowbird (Woodworth 1997). The dissimilarity is related to high cowbird abundance in the southern coastal plain where the species is favored by land uses such as agriculture and cattle ranching. Large pastures in the vicinity of the forest reserve in Guánica (S. Molina-Colón, pers. comm.) contrast to only 4% pastures in 19,382 ha surrounding Maricao (Tossas and Thomlinson 2007). The lower and more open structure of the dry forest in Guánica may also facilitate nest searching by cowbirds.

Differences in reproductive success between PRVIs in Maricao and Guánica may be

affecting the amount of effort invested by pairs in nest building and egg-laying. Pairs in Maricao built new nests after a nesting failure but not after a successful nest. However, pairs in Guánica renested as many as six times after previous failures and also had second broods (Woodworth 1997). This behavior may compensate for high rates of nest loss and low reproductive success. Weather condition may be the ultimate factor affecting the number of nesting attempts and population dynamics overall, as extremely dry conditions have been shown to have a direct relationship with bird population declines in Guánica (Faaborg et al. 1984). Woodworth (1997) found the arrival of rains early in 1991 facilitated rapid initiation of breeding behavior by the PRVI in Guánica with increased opportunities for laying second clutches. That year, six pairs that had fledged young by the beginning of June were able to initiate second broods 1–2 weeks later. In addition to higher chances of reproductive success, nests initiated early in the season were less likely to be parasitized (Woodworth 1997).

Maricao and Guánica can be considered the extremes of a gradient differing in elevation above sea level and habitat characteristics, but aspects of the biology of PRVI were similar in both populations. For example, breeding season lengths at Maricao were similar to those observed in Guánica (106 days in 1991, 69 days in 1993; Woodworth 1997). High levels of nest predation were responsible for nest losses at both sites with 63% of nests at Maricao (this study) and 70% of nests at Guánica (Woodworth 1997) lost to predation. These numbers are typical for open-cup understory nests in the Neotropics, as 67% of nests in wet forests in Costa Rica (Skutch 1985), and 62 and 68% of nests in lowland Panama, in 1996 and 1997, respectively (Robinson et al. 2000) were lost to predation.

The identity of predators could not be ascertained in most cases in the present study, but the lack of damage to the nests suggests birds or reptiles were responsible. Snakes (*Alsophis portoricensis*, *Epicrates inornatus*) that could predate bird eggs or young are uncommon in Maricao, but potential avian predators were frequently observed. The latter include the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*), Pearly-eyed Thrasher (*Margarops fuscatus*), Puerto Rican Lizard Cuckoo (*Coccyzus vieilloti*), and Red-legged Thrush (*Turdus plumbeus*). I cannot dismiss the possibility that nest losses were caused by rodents due to the difficulty of predator identification based on nest damage characteristics (Marini and Melo 1998).

Woodworth (1999) indicated that Guánica is a population sink for the PRVI due to high levels of nest parasitism and depredation. A computer simulation model of the PRVI population with the levels of reproductive success found at Maricao implies this population has a positive growth rate even when the productivity index used in the model is probably an underestimate of the real number of fledglings produced (Tossas 2002). The differences in nest success between the two populations contribute to the idea of a source-sink metapopulation structure, but the short dispersal distances reported for juvenile PRVIs (Woodworth et al. 1998) suggest that Maricao individuals may not migrate as far as Guánica. Alternatively, the surplus of individuals produced at Maricao may disperse to forest fragments surrounding this forest reserve (Tossas and Thomlinson 2007).

Hurricanes directly increase avian mortality rates due to collisions during the storm, or indirectly by destroying the resources on which they depend (Wiley and Wunderle 1993). A study of the impacts of Hurricane Georges in 1998 to the Maricao avian community showed that 16 of 21 species, including the PRVI, declined after the hurricane (Tossas 2006). The reasons for the decline of each species may vary since they have particular ecological requirements and evidence on how resources are affected is scant. Nesting success parameters of PRVI did not vary significantly before and after the hurricane, but a low return rate of color-banded adults was observed in 1999 suggesting that disappearance of individuals was related to the effects of the hurricane. This finding contrasts with the vireo's high return rate and territorial fidelity in a year without a hurricane. Thus, the 1999–2000 annual return rates of 72% was likely typical for the species, while the 39% return estimated from 1998 to 1999 was probably caused by either mortality or dispersal during or immediately after the hurricane. The estimated return in 1999–2000 is similar to the annual survival

probabilities (68–74%) of PRVIs at Guánica reported by Woodworth et al. (1999), Faaborg and Arendt (1995), and Faaborg et al. (1997). The decline in adult return rate resulted in 26% lower density of territorial males the year following the hurricane.

Nest parasitism was not found to threaten the PRVI in this study, but the Shiny Cowbird population may increase at Maricao if hurricanes facilitate their colonization by opening the canopy and altering microhabitat characteristics. Brood parasites and predators may become more abundant if the amount of dense forest in the area surrounding Maricao is affected by fragmentation and deforestation. Changes in land-use practices affecting habitat continuity include rural development by an increased human population and substitution of traditional shade-coffee plantations for sun-grown varieties or other crops with higher yields.

ACKNOWLEDGMENTS

This work was supported by the Department of Biology at the University of Puerto Rico, Río Piedras and grants from the National Science Foundation (Center for Research Excellence in Science and Technology, HRD-9353549; Alliance for Graduate Education and the Professoriate, HRD-9817642). The Puerto Rico Department of Natural and Environmental Resources provided permits to work in Maricao State Forest. Beatriz Hernández and L. A. Muñiz-Campos were helpful in the field. I am grateful to J. M. Wunderle Jr. and R. B. Waide for guidance during the development of the research project, and to B. L. Woodworth for thoughtful reviews of the manuscript. This paper also benefited from comments by J. D. Nichols, E. A. VanderWerf, and two anonymous reviewers.

LITERATURE CITED

Bennett, S. P. and R. Mojica. 1998. Hurricane Georges preliminary storm report: from the tropical Atlantic to the United States Virgin Islands and Puerto Rico. National Weather Service, San Juan, Puerto Rico.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. Mustoe. 2000. Bird census techniques. Second Edition. Academic Press, London, United Kingdom.

Cruz, A., T. Manolis, and J. W. Wiley. 1985. The Shiny Cowbird: a brood parasite expanding its range in the Caribbean region. Ornithological Monographs 36:607–620.

Ewel, J. J. and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Research Paper ITF-18. USDA, Forest Service, Institute of Tropical Forestry, Río Piedras, Puerto Rico.

Faaborg, J. and W. J. Arendt. 1995. Survival rates of Puerto Rican birds: are islands really that different? Auk 112:503–507.

Faaborg, J., W. J. Arendt, and M. S. Kaiser. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a nine year study. Wilson Bulletin 96:575–593.

Faaborg, J., K. M. Dugger, W. J. Arendt, B. L. Woodworth, and M. E. Baltz. 1997. Population declines of the Puerto Rican Vireo in Guánica Forest. Wilson Bulletin 109:195–202.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

Kepler, C. B. and A. K. Kepler. 1970. Preliminary comparison of bird species diversity and density in Luquillo and Guánica forests, Pages E183–191 *in* A tropical rain forest (H. T. Odum, Editor). U.S. Atomic Energy Commission, Oak Ridge, Tennessee, USA.

Krebs, C. J. 1989. Ecological methodology. Harper and Row, Publishers, New York, USA.

Marini, M. Â. and C. Melo. 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. Condor 100:395–399.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Pérez-Rivera, R. A. 1986. Parasitism by the Shiny Cowbird in the interior parts of Puerto Rico. Journal of Field Ornithology 57:99–104.

Purcell, K. L. 2006. Abundance and productivity of Warbling Vireos across an elevational gradient in the Sierra Nevada. Condor 108:315–325.

Raffaele, H. A. 1989. A guide to the birds of Puerto Rico and the Virgin Islands. Princeton University Press, Princeton, New Jersey, USA.

Robinson, W. D., T. R. Robinson, S. K. Robinson, and J. D. Brawn. 2000. Nesting success of understory forest birds in central Panama. Journal of Avian Biology 31:151–164.

Rothstein, S. I. 1990. A model system for coevolution: avian brood parasitism. Annual Review of Ecology and Systematics 21:481–508.

Silander, S., H. Gil de Rubio, M. Miranda, and M. Vázquez. 1986. Los bosques de Puerto Rico. Pages 210–236 *in* Compendio enciclopédico de los recursos naturales de Puerto Rico. Volumen 10. (J. L.Vivaldi, Editor). Departamento de Recursos Naturales, San Juan, Puerto Rico.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Ornithological Monographs 36:575–594.

Tossas, A. G. 2002. Puerto Rican Vireo demography in a montane habitat, with metapopulation implications. Dissertation. University of Puerto Rico, Río Piedras.

Tossas, A. G. 2006. Effects of Hurricane Georges on the resident avifauna of Maricao State Forest, southwestern Puerto Rico. Caribbean Journal of Science 42:81–87.

Tossas, A. G. and J. Thomlinson. 2007. Landscape characteristics of Puerto Rican Vireo (*Vireo latimeri*) nesting habitat, with source-sink implications. Ornitologia Neotropical 18:233–242.

Ward, D. and J. N. M. Smith. 2000. Brown-headed cowbird parasitism in a sink population in Warbling Vireos. Auk 117:337–344.

Wenny, D. G., R. L. Clawson, J. Faaborg, and S. L. Sheriff. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. Condor 95:968–979.

Wiley, J. W. and J. M. Wunderle Jr. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird Conservation International 3:319–349.

Woodworth, B. L. 1997. Brood parasitism, nest predation, and season-long reproductive success of a tropical island endemic. Condor 99:605–621.

Woodworth, B. L. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. Conservation Biology 13:67–76.

Woodworth, B. L., J. Faaborg, and W. J. Arendt. 1998. Breeding and natal dispersal in the Puerto Rican Vireo. Journal of Field Ornithology 69:1–7.

Woodworth, B. L., J. Faaborg, and W. J. Arendt. 1999. Survival and longevity of the Puerto Rican Vireo. Wilson Bulletin 111:376–380.

The Wilson Journal of Ornithology 120(3):467–472, 2008

NEST DEFENSE BY CAROLINA WRENS

KELLY A. D'ORAZIO[1,2] AND DIANE L. H. NEUDORF[1,3]

ABSTRACT.—We examined nest defense behavior of the Carolina Wren (*Thryothorus ludovicianus*) in response to avian intruders at the nest. Freeze-dried mounts of a brood parasite (female Brown-headed Cowbird [*Molothrus ater*]), nest predator (Blue Jay [*Cyanocitta cristata*]), and a control (Swainson's Thrush [*Catharus ustulatus*]) were presented at wren nests to examine if wrens were able to distinguish among these threats. The primary nest defense behavior of Carolina Wrens was alarm calls. Wrens spent more time alarm calling to the Blue Jay model than the control and Brown-headed Cowbird models suggesting cowbirds were not recognized as threats to the nest. Wrens were less likely to respond during laying stage trials, probably due to a lack of nest visitations at this time. Intensity of alarm calls did not increase from the laying to nestling stage for any of the models presented. Carolina Wrens are both socially and genetically monogamous, and males should invest heavily in care of young due to their high confidence of paternity. Males and females did not differ in the amount of time spent alarm calling to any of the models, and defended their nests from intruders with equal intensity as predicted by the confidence of paternity hypothesis. *Received 21 October 2006. Accepted 4 October 2007.*

Nest defense is a common behavior used by birds to improve survival of their young in an attempt to increase the potential of passing their genes on to future generations. Nest defense can be costly and parents are expected to make an optimal compromise between their own safety and that of their young (Andersson et al. 1980). Responses of nest owners are expected to be influenced by the reproductive value of their young and the stimulus value of the intruder (Patterson et al. 1980). Thus, parents should respond selectively to intruders that pose the most threat in conjunction with timing of the nesting cycle and the expected future benefits of survival of young.

The two main causes of nesting failure in songbirds are predation (Wilcove 1985, Martin 1992, Robinson 1992) and brood parasitism (Mayfield 1977, Brittingham and Temple 1983, Robinson et al. 1995). Predation is responsible for loss of over 50% of eggs and nestlings in some passerine species (Ricklefs 1969). Hosts of the parasitic Brown-headed Cowbird (*Molothrus ater*) have reduced nesting success because of removal or damage to their eggs, and nestling or fledgling death from competition (Friedmann 1963, Rasmussen and Sealy 2006). Cowbirds also depredate nests by destroying eggs or killing nestlings (e.g., Friedmann 1929, Du Bois 1956, Granfors et al. 2001, Smith et al. 2003).

Carolina Wrens (*Thryothorus ludovicianus*) are a non-migratory songbird of the eastern United States and portions of Central America (Haggerty and Morton 1995). Brood parasitism of the Carolina Wren by the Brown-headed Cowbird has previously been documented (Bent 1948, Mengel 1965, Woodward 1983, Haggerty and Morton 1995). Carolina Wrens are recognized as an acceptor of cowbird eggs and can raise fledglings to independence (Woodward 1983). However, little is known about the wren's nest defense behavior toward cowbirds during their breeding season.

We quantified nest defense behavior of the Carolina Wren in response to models of a: (1) female Brown-headed Cowbird, (2) Blue Jay (*Cyanocitta cristata*) (an avian nest predator), and (3) Swainson's Thrush (*Catharus ustulatus*) (a non-threatening species), during the egg-laying and nestling stages. We predicted that wrens would increase their level of defense towards an avian nest predator over the nesting cycle as young increased in value to the parents. Responses to the female cowbird model are predicted to be most intense at the laying stage when parasitism is a threat (e.g., Neudorf and Sealy 1992). Alternatively, if wrens view cowbirds as nest predators, responses to the cowbird model should also be intense at the nestling stage. We compared the responses of males and females to each intruder to examine if parents differed in their responses. Carolina Wrens are both socially

[1] Department of Biological Sciences, Sam Houston State University, Huntsville, TX 77341, USA.

[2] Current address: 792 East Cowboy Cove, Queen Creek, AZ 85242, USA.

[3] Corresponding author; e-mail: neudorf@shsu.edu

and genetically monogamous (Haggerty et al. 2001); males have a high confidence of paternity and should invest heavily in offspring care. Thus, we predicted that both males and females would defend their nests with equal intensity (Hobson et al. 1988, Montgomerie and Weatherhead 1988).

METHODS

Study Site.—This study was conducted from March-August 2001 through 2003 on and around Sam Houston State University's Center for Biological Field Studies, Huntsville, Texas. The 100-ha area (30° 74′ N, 95° 48′ W) provides abundant habitat for Carolina Wrens, which are year-round residents at the field station. Habitat includes mixed pine (*Pinus* spp.)-hardwood forests, open prairie inclusions, old-field succession, and riparian areas along two creeks (Dent and Lutterschmidt 2001).

Nest Monitoring and Banding.—Carolina Wrens nest in both natural and artificial sites (Haggerty and Morton 1995) that provide a suitable cavity. We constructed 120 nest boxes and placed them in appropriate habitats, and within known territories, to entice the birds to nest. Boxes were checked every 2–3 days for signs of nesting activity.

Males and females are nearly identical in plumage, but males often have greater mass with longer bills, wings, and legs (Haggerty and Morton 1995). Most individuals were captured with mist nets coupled with song or call playback, uniquely color banded, and released. Gender was assigned by the presence or absence of a brood patch or cloacal protuberance, and vocalizations.

Model Presentation.—Freeze-dried mounts of a female Brown-headed Cowbird, Blue Jay, and Swainson's Thrush were presented at wren nests to quantify nest defense. Mounts were prepared with glass eyes and made to appear life-like. We used only one model of each of the three species we presented. These were salvaged specimens and should represent a random individual from each species. The mounts remained in good condition over the course of the study because wrens did not physically contact them.

A thrush was chosen as a control because it is similar in size, shape, and coloration to the female cowbird. Thrushes are migrants through the study area and pose no threat to wrens. The Blue Jay is larger than the other two model species, but is the smallest known avian predator of eggs and nestlings that is also abundant in the study area.

Models were wired to an alligator clip attached to a moveable perch to allow ease of manipulation during testing. The perch was placed 1 m from the nest and positioned with the mount facing the nest opening. Presentations of models were in random order and each nest was tested only once per breeding season.

Observations.—Procedures for nest defense testing generally followed Sealy et al. (1998). All observations were conducted by a single individual (KAD) for consistency and nests were tested between 0700 and 1100 hrs (CST). Laying stage observations were conducted anytime after the first egg was produced until the penultimate egg was laid. Carolina Wren clutch size is typically four eggs that are laid on successive days within 1–2 hrs of sunrise (Haggerty and Morton 1995). Nestling stage observations were conducted on nests containing 5 to 11 day-old nestlings. Observations were made from a blind 5–10 m from the nest as surrounding vegetation allowed. The blind and perch were positioned at least 1 day prior to testing to allow birds to habituate to these objects near their nests. The observer hid in the blind until the mated pair was away from the nest and then positioned models on the perch and returned to the blind. The 5-min trial commenced when we observed either bird return. Each model was presented for a 5-min trial with at least a 15-min rest period between presentations. The model was immediately removed after a trial and the observer returned to the blind. We found 15 min to be sufficient to allow for birds to stop responding and resume normal activity after a model was removed. We did not put the next model in place if the parents were still at the nest after 15 min until they left the area. Observations during testing were recorded on a portable cassette recorder and later transcribed.

Three commonly used alarm calls including female "rasp", female "dit", male "ti-dink" and male "rasp" (Haggerty and Morton 1995) were observed in response to models. All calls were quantified as the number of 10-sec in-

TABLE 1. Alarm calls of Carolina Wrens to models during egg-laying and nestling stages.

Response[a]	Model		
	Cowbird	Blue Jay	Thrush
Egg laying	4.9 ± 3.7 $n = 5$	15.2 ± 4.0 $n = 9$	3.6 ± 2.4 $n = 6$
Nestling	6.6 ± 1.8[b] $n = 16$	17.2 ± 2.1[c] $n = 16$	6.0 ± 2.2[b] $n = 16$
t[d]	0.45	0.44	0.62
P	0.66	0.67	0.54

[a] Responses are given as the mean ± SE. Alarm calls were measured as the number of 10-sec intervals that wrens responded. Responses were averaged when two wrens responded.

[b, c] Results of Bonferroni multiple comparison test (nestling stage only) examining differences in responses between models. Means with different superscripts differed significantly.

[d] Two-sample t-tests to compare responses between nest stages. All tests were two-tailed.

tervals in which they occurred during model presentation (maximum of 30 for a 5-min trial). Any aggressive behaviors such as close passes (flying within 0.5 m above the model) or strikes at the models were also noted. A bird was given a zero for the alarm call category if it returned to the nest but did not vocalize. The next model was put in place after a 15-min rest period if no birds were observed returning to the nest. The trial was considered a "no response" after 1 hr and the model was removed. The visibility of returning adults to the observer was limited to 5–10 m around the nest depending on the surrounding vegetation. It is possible that if a bird returned and sat quietly at a distance it may not have been seen by the observer.

Statistical Analyses.—Statistical comparison of wren alarm calls among models within the same nesting stage was only possible for the nestling stage due to the number of no responses during several trials at the egg laying stage. Different alarm calls for males and females were combined into one alarm call category to facilitate analysis. The results were averaged if two individuals responded to a given model. A repeated measures ANOVA was performed to detect differences in nest defense behavior to presented models at the nestling stage. Significant results ($P < 0.05$) were analyzed by Bonferroni's multiple comparison test to identify those models that elicited significantly different responses. We used a two-sample t-test to compare nest defense responses between nest stages for each model.

A paired t-test was used to analyze differences between responses of males and females for each model. We used trials only where both members of the pair responded to a particular model. Gender responses were compared only at the nestling stage due to the low number of individuals responding at the laying stage. Chi-square or Fisher's exact tests were used to compare the number of males and females that responded among models. All values are reported as mean ± SE and all tests were two-tailed. Data were analyzed with GraphPad Prism 4.0 or StatView 4.5 software.

RESULTS

The primary nest defense response of Carolina Wrens to model intruders at the nest was alarm calls. Only one female made a close pass at each model during a nestling stage trial and no strikes were observed. It was not unusual for pairs to feed nestlings before or after giving alarm calls at the nest.

Discrimination Among Models.—Discrimination among models at the laying stage was difficult to assess due to lack of parental response. However, the data suggest a stronger response to the Blue Jay model (Table 1). Time spent alarm calling at the nestling stage was greatest toward the Blue Jay model (repeated measures ANOVA, $F_{2,30} = 11.9$, $P = 0.0002$; Table 1). Time spent alarm calling did not increase significantly over the nesting cycle for any of the models (Table 1).

Differences Between Male and Female Responses.—The number of 10-sec intervals spent alarm calling did not differ at the nestling stage between males and females in response to the Blue Jay model (male: 17.0 ± 2.9, female: 16.0 ± 3.3; paired t-test = 0.21, df = 12, $P = 0.83$) or the thrush model (male: 11.1 ± 3.6, female: 8.5 ± 4.5; paired t-test, $t = 0.58$, df = 7, $P = 0.58$). Females spent more time alarm calling to the cowbird model than did males but this difference was not sig-

nificant (male: 5.2 ± 2.3, female: 13.2 ± 3.6; $t = 1.91$, df = 10, $P = 0.09$).

Male (2, 5, and 1) and female (5, 9, and 4) Carolina Wrens ($n = 15$ nests tested during the egg-laying stage) responded to the cowbird, Blue Jay, and thrush models, respectively. Females appeared to respond more than males at the laying stage but differences were not significant (Fisher exact test, NS; comparing responses to thrush and Blue Jay models). Sixteen nests were tested during the nestling stage and 12, 14, and 13 males and 12, 14, and 13 females responded to the cowbird, Blue Jay, and thrush models, respectively. Males and females responded in similar numbers at the nestling stage to all three models ($\chi^2 = 0.321$, df = 2, $P = 0.85$).

DISCUSSION

Carolina Wrens relied on alarm calls as their primary defense. Their use of vocalizations as a defensive system occasionally alerted other species of birds in the area which congregated near the model resulting in a mobbing response. Mobbing may function to let a predator know it has been discovered and cause it to leave the area (Curio 1978). Carolina Wrens in an adjacent territory responded to the alarm calls of the nest owners during only one observation.

Carolina Wrens often did not respond to model trials at the laying stage. Models in several instances were left in place for 1 hr and no birds were observed anywhere near the nest area. This is likely due to a lack of nest visitations by wrens during the laying stage rather than birds hiding from the observer's view. Nice and Thomas (1948) reported few nest visitations by a pair of Carolina Wrens during the laying stage. Most observed visits were early in the morning and associated with egg laying. We found no difference among models in the number of males and females responding at the laying stage. We would expect lower numbers of males and females responding to the Blue Jay model than the thrush model if birds were hiding out of sight to avoid attracting a predator to the nest. Birds may reduce visits to their nests to avoid attracting attention of predators or brood parasites and leading them to the nest (McLean 1987, Eggers et al. 2005). This could account for the low numbers of individuals responding at the laying stage in our study. However, when wrens did respond at the laying stage their level of response was similar to the nestling stage (Table 1).

Recognition of Threats.—Carolina Wrens recognized and defended their nests from the model of the Blue Jay, a common nest predator on our study site (Table 1). The intensity of nest defense by wrens in response to the Blue Jay model did not increase as the nesting cycle progressed from egg-laying to nestling stage. Parents are expected to increase responses to predators over the nesting cycle according to the reproductive value hypothesis (Andersson et al. 1980, Patterson et al. 1980). This hypothesis has been supported in several studies of songbirds (Greig-Smith 1980, Westneat 1989, Burhans 2001). However, other studies did not find the predicted increase in nest defense over the nesting cycle (Knight and Temple 1986) or did not find an increase in all species examined (Neudorf and Sealy 1992). The primary nest defense behavior of Carolina Wrens was alarm calls, which is presumably a lower risk activity to parents than close passes or strikes. The risk of injury from the much larger Blue Jay may have outweighed the potential benefits of increased aggression at the nestling stage.

Level of alarm calling to the cowbird model was similar to that of the control suggesting wrens do not recognize cowbirds as a significant threat. There are no records of Brown-headed Cowbird parasitism of Carolina Wrens in our study area ($n = 118$ nests over 6 years; D. L. H. Neudorf, unpubl. data) perhaps because wrens use nest boxes that are too small and enclosed for cowbirds. Many birds recognize cowbirds as threats to their nests (e.g., Song Sparrows [*Melospiza melodia*], Smith et al. 1984; Red-winged Blackbirds [*Agelaius phoeniceus*], Neudorf and Sealy 1992; Hooded Warblers [*Wilsonia citrina*], Mark and Stutchbury 1994; Yellow Warblers [*Dendroica petechia*], Gill and Sealy 1996). However, these species are more common cowbird hosts and presumably have more opportunities to interact with cowbirds.

Differences in Responses of Males and Females.—Male and female Carolina Wrens defended their nests from the models with equal intensity at the nestling stage. Neither differed in propensity to respond nor amount of time

spent alarm calling to the models. Differences between males and females in nest defense are not uncommon in birds and can be attributed to many factors (Montgomerie and Weatherhead 1988). Generally, females have a higher confidence of parenthood (Trivers 1972) and should take more risks in an effort to increase their fitness (Montgomerie and Weatherhead 1988). Carolina Wrens are socially monogamous and extra-pair copulations apparently do not occur in this species (Haggerty et al. 2001). Thus, it appears parental care in the form of nest defense is shared equally in Carolina Wrens supporting the confidence of paternity hypothesis.

ACKNOWLEDGMENTS

We are grateful to Jana Story and Anne Domonoske for assistance during the 2001 field season. T. M. Haggerty provided advice on nest box design. Everett Wilson generously constructed nest boxes. Keith Arnold and William Armstrong donated bird specimens for models. Robert Rhodes provided assistance with freeze-drying. Colleen Barber and two anonymous reviewers provided comments on the manuscript. Funding was provided by Sam Houston State University (SHSU), Department of Biological Sciences Research Award (2001 and 2002 to KAD) and a SHSU Research Endowment Fund Grant (2001 to DLHN).

LITERATURE CITED

Andersson, M., C. G. Wiklund, and H. Rundgren. 1980. Parental defense of offspring: a model and an example. Animal Behaviour 28:536–542.

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. National Museum Bulletin 195.

Brittingham, M. C. and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33:31–35.

Burhans, D. E. 2001. Enemy recognition by Field Sparrows. Wilson Bulletin 113:189–193.

Curio, E. 1978. The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. Zeitscrift Tierpsychologie 48:175–183.

Dent, L. and W. I. Lutterschmidt. 2001. The ichthyofauna of Harmon and Wynne creeks sampled within the Center for Biological Field Studies, Walker County, Texas. Texas Journal of Science 53:139–146.

Du Bois, A. D. 1956. A cowbird incident. Auk 73: 286.

Eggers, S., M. Griesser, and J. Ekman. 2005. Predator-induced plasticity in nest visitation rates in the Siberian Jay (*Perisoreus infaustus*). Behavioral Ecology 16:309–315.

Friedmann, H. 1929. The cowbirds: a study in the biology of social parasitism. C. C. Thomas, Springfield, Illinois, USA.

Friedmann, H. 1963. Social parasitism in birds. Quarterly Review of Biology 3:554–569.

Gill, S. A. and S. G. Sealy. 1996. Nest defense by Yellow Warblers: recognition of a brood parasite and an avian nest predator. Behaviour 133:263–282.

Granfors, D. A., P. J. Pietz, and L. A. Joyal. 2001. Frequency of egg destruction by female Brown-headed Cowbirds at grassland nests. Auk 118: 765–769.

Greig-Smith, P. W. 1980. Parental investment in nest defense by Stonechats (*Saxicola torquata*). Animal Behaviour 28:604–619.

Haggerty, T. M. and E. S. Morton. 1995. Carolina Wren (*Thryothorus ludovicianus*). The birds of North America. Number 188.

Haggerty, T. M., E. S. Morton, and R. C. Fleischer. 2001. Genetic monogamy in Carolina Wrens (*Thryothorus ludovicianus*). Auk 118:215–219.

Hobson, K. A., M. L. Bouchart, and S. G. Sealy. 1988. Reponses of naïve Yellow Warblers to a novel nest predator. Animal Behaviour 36:1823–1830.

Knight, R. L. and S. A. Temple. 1986. Why does intensity of avian nest defense increase during the nesting cycle? Auk 103:318–327.

Mark, D. and B. J. Stutchbury. 1994. Response of a forest-interior songbird to the threat of cowbird parasitism. Animal Behaviour 47:275–280.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Editors). Smithsonian Institute Press, Washington, D.C., USA.

Mayfield, H. 1977. Brown-headed Cowbird: agent of extermination. American Birds 31:107–113.

McLean, I. G. 1987. Response to a dangerous enemy: should a brood parasite be mobbed? Ethology 75: 235–245.

Mengel, R. M. 1965. The birds of Kentucky. Ornithological Monographs 3.

Montgomerie, R. D. and P. J. Weatherhead. 1988. Risks and rewards of nest defense by parent birds. Quarterly Review of Biology 63:167–187.

Neudorf, D. L. and S. G. Sealy. 1992. Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized responses? Behaviour 123:85–105.

Nice, M. M. and R. H. Thomas. 1948. A nesting of the Carolina Wren. Wilson Bulletin 60:139–158.

Patterson, T. L., L. Petrinovich, and D. K. James. 1980. Reproductive value and appropriateness of response to predators by White-crowned Sparrows. Behavioral Ecology and Sociobiology 7: 227–231.

Rasmussen, J. L. and S. G. Sealy. 2006. Hosts feeding only Brown-headed Cowbird fledglings:

where are the host fledglings? Journal of Field Ornithology 77:269–279.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9: 1–48.

Robinson, S. K. 1992. Population dynamics of breeding neotropical migrants in a fragmented Illinois landscape. Pages 408–418 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Editors). Smithsonian Institute Press, Washington, D.C., USA.

Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995. Ecology and behavior of cowbirds and their impact on host populations. Pages 428–460 *in* Ecology and management of neotropical migratory birds (T. E. Martin and D. Finch, Editors). Oxford University Press, New York, USA.

Sealy, S. G., D. L. Neudorf, K. A. Hobson, and S. A. Gill. 1998. Nest defense by potential hosts of the Brown-headed Cowbird: methodological approaches, benefits of defense, and coevolution. Pages 194–211 *in* Parasitic birds and their hosts: studies in coevolution. (S. I. Rothstein and S. K. Robinson, Editors). Oxford University Press, New York, USA.

Smith, J. N. M., P. Arcese, and I. G. McLean. 1984. Age, experience, and enemy recognition by wild Song Sparrows. Behavioral Ecology and Sociobiology 14:101–106.

Smith, J. N. M., M. J. Taitt, L. Zanette, and I. H. Myers-Smith. 2003. How do Brown-headed Cowbirds (*Molothrus ater*) cause nest failures in Song Sparrows (*Melospiza melodia*)? A removal experiment. Auk 120:772–783.

Trivers, R. L. 1972. Parental investment and sexual selection. Pages 139–179 *in* Sexual selection and the descent of man (B. Campbell, Editor). Aldine, Chicago, Illinois, USA.

Westneat, D. F. 1989. Intensity of nest defense in Indigo Buntings increases with stage and not number of visits. Auk 106:747–749.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

Woodward, P. W. 1983. Behavioral ecology of fledgling Brown-headed Cowbirds and their hosts. Condor 85:151–163.

The Wilson Journal of Ornithology 120(3):473–477, 2008

NEST, EGGS, AND PARENTAL CARE OF THE PUNA TAPACULO (*SCYTALOPUS SIMONSI*)

PETER A. HOSNER[1,3] AND NOEMÍ E. HUANCA[2]

ABSTRACT.—We describe the nest and eggs of the Puna Tapaculo (*Scytalopus simonsi*) from Bolivia, and include observations of nest building, incubation, and parental care. The nest is similar to several other described nests in the genus in construction and placement: a domed cup nest of grasses in an excavated burrow in a vertical bank. Both male and female constructed the nest, brooded, and provisioned the young, typical of *Scytalopus* and tracheophone suboscines. This is only the second described *Scytalopus* nest constructed of grasses, probably an adaptation to its drier habitat near and above treeline. The growing body of *Scytalopus* nest descriptions suggests they do not exhibit generic level stereotyped nest structure and placement, unlike other tracheophone suboscines, which show strong phylogenetic signal in nest architecture. *Received 1 September 2007. Accepted 26 January 2008.*

Scytalopus is among the most diverse and abundant groups of Andean birds, yet their breeding biology is poorly understood. Nests of 15 of the 41 (Gill and Wright 2006, Remsen et al. 2008) currently recognized species of *Scytalopus* have been described, all of which share similarities but differ somewhat in placement or structure. The nest site is usually some form of natural crevice or cavity (Skutch 1972, Hilty and Brown 1986, De Santo et al. 2002, Acros-Torres and Solano-Ugalde 2007), excavated burrow in an earthen bank (Johnson and Goodall 1965, Stiles 1979, Young and Zuchowski 2003, Decker et al. 2007, Pulgarin-R 2007), cavity in a rotten log (Greeney and Gelis 2005), or hidden among dense foliage, roots, trunks, fallen leaves, and moss (Rosenberg 1986, Sick 1993, Christian 2001). Nest architecture in *Scytalopus* approaches the entire range of variation of all the rhinocryptids (Krabbe and Schulenberg 2003) and nests usually are domed or globular in shape with a top or side entrance; only nests of White-browed Tapaculo (*S. superciliaris*) (Stiles 1979) and Long-tailed Tapaculo (*S. micropterus*) (Greeney et al. 2005) have been found with an open cup. Nests are constructed from a variety of plant material including mosses, lichens, rootlets, leaves, small sticks, and are at times lined with grasses, hair, or feathers (Krabbe and Schulenberg 2003).

Field observations of *Scytalopus* during the breeding period are extremely limited. Males lack a brood patch (Krabbe and Schulenberg 2003), but incubation has been reported by both males and females (Young and Zuchowski 2003, Decker et al. 2007), as has brooding (Greeney et al. 2005). The incubation period has been reported to be from 15 (Sick 1993) to 19 days (DeSanto et al. 2002); the only recorded fledging period is 11 days (DeSanto et al. 2002). Both parents actively provision the chicks with small arthropods (Christian 2001, Young and Zuckowski 2003, Greeney and Gelis 2005, Greeney and Rombough 2005, Greeney et al. 2005). Nothing is recorded on nest building or post fledging care (Krabbe and Schulenberg 2003).

The Puna Tapaculo (*Scytalopus simonsi*) occurs at high elevations (2,000–4,500 m) in Puna grassland, ravines with shrubby vegetation, *Polylepis* woodland, and elfin forest edge from Departamento Cuzco, Peru south to Departamento Santa Cruz, Bolivia (Hennessey et al. 2003, Krabbe and Schulenberg 2003). Once considered conspecific with Magellanic Tapaculo (*S. magellanicus*) (i.e., Zimmer 1939), differences in song, distribution, and morphology have split this complex into 11 recognized species with further taxonomic revisions likely (Remsen et al. 2008). The objectives of this paper are to describe the nest, eggs, and parental care in *S. simonsi*, and discuss trends in *Scytalopus* breeding behavior.

OBSERVATIONS

On 16 December 2006 near the community of Palcapampa (17° 20′ S, 66° 24′ W; 3,550

[1] Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA.

[2] Asociacíon Armonia, Santa Cruz de la Sierra, Santa Cruz, Bolivia.

[3] Corresponding author; e-mail: hosner@ku.edu

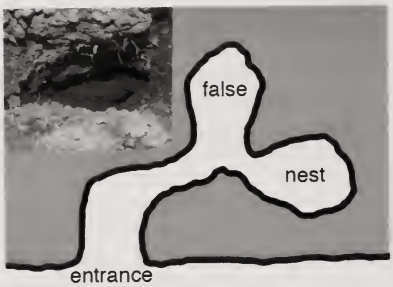


FIG. 1. Schematic of nest burrow of Puna Tapaculo showing the false and nest chambers. Photograph of entrance hole (inset).

FIG. 2. Nest cup of Puna Tapaculo after extraction from the burrow; the dome could not be extracted for photographs. The two eggs (inset).

m), Departamento Cochabamba, Bolivia, we observed a *Scytalopus simonsi* hopping across a footpath carrying grasses. The bird (presumed to be a female as it lacked a white postocular line) re-crossed the footpath after 30 sec and hopped up a steep bank, disappearing into one of about nine burrows. When we retuned to the site on 17 December 2006, a *S. simonisi* was peering from the entrance of the nest hole (presumed to be the male of the pair based on the distinctive short whitish post-ocular stripe). The bird exited, dropped to the ground and crept away. The bank was 2.5 m tall and was constructed as a terrace between two small potato fields. The bank was almost vertical, sloping gradually to horizontal as it met the lower field. The nest hole was in plain view, 20 cm below the top of the bank, which was covered with grasses and other herbaceous vegetation. There was a small (15 m wide, 3 m deep) ravine 20 m from the nest site with *Alnus acuminata*, *Polylepis besserii*, and other native shrubs including *Gynoxis*, *Baccharis*, *Ribes*, and *Berberis*, and *Festuca* and *Cortaderia* grasses, a more typical habitat of the species. The male was heard singing there infrequently (a few songs per hour) during investigation of the nest.

The entrance hole (Fig. 1) measured 9 × 4 cm, the only oval hole among many circular holes of various sizes in the bank. The burrow (Fig. 1) went straight into the bank 18 cm, tapering slightly before turning sharply 80° to the right, narrowing to 7 × 4.5 cm, and continuing another 16 cm before opening into two chambers: one empty to the left, and one to the right which contained the nest. A few rootlets from herbaceous vegetation emerged from the ceiling of the burrow. The nest was in an area replete with rodent burrows (9 other holes within a few meters of the nest). The entrance to the nest chamber was oval, measuring 10 × 8 cm, the nest chamber itself was almost spherical at 12 × 12 × 18 cm. The sides and ceiling of the chamber were lined with ~4 cm of loosely woven dried *Cortaderia* grasses that formed a dome over the nest.

The nest cup (Fig. 2) was 12 cm in diameter and 10 cm in height, filling the lower two-thirds of the nest chamber. The walls and bottom of the cup were lined with 3.5 cm of much more tightly woven grasses than the loose dome. Five blades of *Cortaderia* grass taken at random from the nest cup measured 5, 7, 8, 12, and 17 cm in length; all grasses were about 0.5 mm in width. The cup had an inside diameter of 5 cm and inside depth of 6.5 cm. The lining of the interior of the cup was of much smaller, finer grasses than the rest of the nest and included a few long black horse hairs, several species of bird feathers including domestic chicken (*Gallus gallus*), and a single piece of moss. The nest was clean and devoid of droppings upon extraction.

The nest contained two eggs that were cold on 17 December 2007, although the male was in attendance. The eggs were white, the eggshells seemed thin and had a transparent quality; the air sac at the large end of the egg was easily visible. Eight sets of transparent parallel lines 2 mm apart went half the length of the eggs, converging at the small tip. Egg #1 measured 23.30 × 17.60 mm, weighing 3.9 g; egg #2 measured 23.36 × 17.26 mm and weighed 3.8 g. The male continued to bring stems of grass to the nest after the eggs were replaced.

The eggs hatched by 4 January and the

chicks were estimated to be 2 days of age, weighing 4.5 and 4.9 g with nare to tip of bill measurements of 3.8 and 3.9 mm. Assuming incubation began on 18 December 2007, the day after the two eggs were found to be cold, the incubation period would have been 16 days. The chicks retained the egg tooth, had eyes closed, and were partially covered with long, thick mouse gray natal down on the crown, back, wings, and legs. After the chicks were returned to the nest, the female brooded for 27 min. The male arrived with food and the pair switched with the male staying to brood. The pair alternated brooding and foraging 33% of the time observed. The brooding bird would stay in the nest until the other returned with food, then exited allowing the provisioning bird to enter, feed the chicks, and brood the nestlings. The female made six foraging bouts and the male four from 1500 to 1630 hrs CST. The food brought by the adults appeared to be a mix of ~50% small (~10 mm) insect larvae and 50% (~5–10 mm) small adult insects with one small white moth (~10 mm). The female spent 34 min of the 1.5 hrs brooding and at dusk spent the night brooding in the nest. The male spent 16 min brooding during this period and roosted at night in nearby shrubs.

The chicks weighed 5.7 and 6.2 g on 6 January 2007, and provisioning behavior by the adults was similar although they spent little time brooding, and exited the nest directly after feeding rather than waiting for the arrival of their mate. The female made seven foraging bouts, the male four in 1.15 hrs of observation. Adults entered the nest hole three times but were not identified to gender. Begging calls of the chicks were recorded (ML #132524) by placing a microphone inside the nest for 30 min during active feeding. The chicks called (soft high pitch peeping) almost continuously in the presence and absence of adults. Provisioning behavior was similar in 30 min of observation on 7 January 2007 and both adults were observed removing fecal sacs from the nest for the first time.

The chicks were covered in pin feathers on 14 January 2007, although their eyes were still closed and they retained some natal plumes on the crown and back. The majority of the feathers on the back had lost their pins and were brown with thick black barring typical of all juvenile *Scytalopus*. The chicks weighed 18.1 and 19.8 g, had nare to tip of bill measurements of 6.2 and 6.3 mm, and tarsi of 19.7 and 20.4 mm. The nest was empty on 6 February and was removed from the cavity. The fledging period was >12 days and, given the stage of development at 12 days, a fledging period of 15–20 days seems reasonable.

DISCUSSION

Given the identification issues and taxonomic changes in this genus (i.e., Krabbe and Schulenberg 1997), a recording of the male at the nest was deposited at the Macaulay Library at Cornell University (ML #132525). Young and Zuchowski (2003) erroneously cited a nest of *S. simonsi* found by T. S. Schulenberg in Puno, Peru (Rosenberg 1986). This nest correctly pertains to Diademed Tapaculo (*S. schulenbergi*) (Krabbe and Schulenberg 2003; T. S. Schulenberg, pers. comm.).

The domed nest was similar in structure to other *Scytalopus* nests; however, use of bunch grasses as construction material has been previously reported only in *S. superciliaris* (Stiles 1979). Use of bunch grasses is probably an adaptation for living in areas above treeline where it is one of the only nesting materials available. Mosses were available at the site, although in much less quantity than the extremely humid subtropical and temperate mossy forests where the majority of the *Scytalopus* nests have been described. This pair of *S. simonsi* also used a longer tunnel than previously described for nests of the genus; however, the growing number of *Scytalopus* nest descriptions suggests the genus is extremely variable and opportunistic in selecting a nest site. They apparently use a variety of structures for nest sites and, perhaps, vary nest architecture based upon the individual nest site (Greeney and Gelis 2005, Greeney 2008), rather than stereotyped nest architecture with a genetic basis (i.e., Zyskowski and Prum 1999, Zimmer and Isler 2003, Brumfield et al. 2007) seen in other tracheophone groups. It appears likely the nest burrow was modified from an old rodent excavation and that rodents, rather than *Scytalopus*, constructed the false chamber and nest chambers. Alternatively, the shape of the entrance resembled the burrow of Bar-winged Cinclodes (*Cinclodes*

fuscus) and it could have been a re-used burrow of that species. Recently, Greeney (2008) described the first unambiguously re-used nest by a *Scytalopus*, the Long-tailed Tapaculo, which had taken over a nest built and used to raise three broods by a pair of Spotted Barbtails, (*Premnoplex brunnescens*).

Parental care of the chicks was typical for the genus (Greeney and Gelis 2005, Greeney and Rombough 2005, Greeney et al. 2005) with both parents contributing to virtually all activities. The sexual dimorphism in *S. simonsi* allowed for our novel observations that males also contribute to nest building, and that while the male actively contributed to feeding and brooding, it provisioned slightly less frequently and spent less time brooding than the female. The used nest devoid of fecal sacs from the chicks suggests that, like in other nests (Greeney and Gelis 2005, Greeney and Rombough 2005), *S. simonsi* chicks may excrete outside of the nest and the parents keep the nest extraordinarily clean. The appearance of the chicks and unique natal down were typical of *Scytalopus* (Greeney and Gelis 2005). However, the soft peeping calls of the chicks differed strongly from previous descriptions (Greeney and Gelis 2005) that *Scytalopus* chick vocalizations were loud and insect or woodpecker-like. Whether this is due to the young age of the *S. simonsi* chicks or interspecific differences is unknown. Incubation in *S. simonsi* appears much longer than that of *magellanicus* (DeSanto et al. 2002), but exact dates of laying and hatch are unknown.

Little is known about the post-fledgling care of *Scytalopus* and we were unable to observe the birds post fledging. PAH frequently observed a pair of *S. parkeri* at Reserva Tapichalaca in Loja, Ecuador accompanying and provisioning a single fledgling in the same territory for 3 weeks from mid October through early November 2005. This suggests a long period of post-fledging care by adults in the group, much as in related tracheophone families (Zimmer and Isler 2003).

Many aspects of *Scytalopus* breeding behavior (i.e., shared nest building, shared incubation although only the female incubates at night, shared provisioning of young, extended parental care after fledging, and low rates of nest success) appear similar to the other tracheophones. We hypothesize that *Scytalopus* are also similar to tracheophones in their monogamy, extended pair bonds, and other aspects of breeding biology yet to be studied or observed in this fascinating group.

ACKNOWLEDGMENTS

We thank the American Bird Conservancy for financing the study on Cochabamba Mountain Finch (*Compospiza garleppi*) during which we made these observations. We also thank Asociación Civil Armonía/BirdLife International and the communnities of Palcapampa and Portrero for allowing access to the study areas and providing support. The Macaulay Library at Cornell University loaned recording equipment. The Herbario Nacional Martín Cárdenas assisted in plant identification. A. B. Hennessey, S. K. Herzog, Luis Llanos, Felix Huanca, Israel Huanca, and Josias Huanca assisted with logistics and fieldwork. M. B. Robbins provided comments that improved the manuscript.

LITERATURE CITED

Acros-Torres, A. and A. Solano-Ugalde. 2007. First description of the nest, nest site, eggs, and nestlings of Narino Tapaculo (*Scytalopus vicinior*). Ornitologia Neotropical 18:445–448.

Brumfield, R. T., J. G. Tello, Z. A. Cheviron, M. D. Carling, N. Crochet, and K. V. Rosenberg. 2007. Phylogenetic conservation and antiquity of a tropical specialization: army-ant following in the typical antbirds (Thamnophilidae). Molecular Phylogenetics and Evolution 45:1–13.

Christian, D. G. 2001. Nests and nesting behavior of some little known Panamanian birds. Ornitología Neotropical 12:327–336.

Decker, K. L., A. M. Niklison, and T. E. Martin. 2007. First description of the nest, eggs, and breeding behavior of the Merida Tapaculo (*Scytalopus meridanus*). Wilson Journal of Ornithology 119:121–124.

De Santo, T. L., M. F. Willson, K. E. Sieving, and J. J. Armesto. 2002. Nesting biology of tapaculos (Rhinocryptidae) in fragmented south-temperate rainforests of Chile. Condor 104:482–495.

Gill, F. and M. Wright. 2006. Birds of the world. Recommended English names. Princeton University Press, Princeton, New Jersey, USA and Oxford, United Kingdom.

Greeney, H. F. 2008. Additions to our understanding of *Scytalopus* tapaculos reproductive biology. Ornitología Neotropical 19: In press.

Greeney, H. F. and R. A. Gelis. 2005. The nests and nestlings of the Long-tailed Tapaculo (*Scytalopus micropterus*) in Ecuador. Ornitología Colombiana 3:88–91.

Greeney, H. F. and C. J. F. Rombough. 2005. First nest of the Chusquea Tapaculo (*Scytalopus parkeri*) in southern Ecuador. Ornitología Neotropical 16:439–440.

Greeney, H. F., A. D. L. Buecker, and N. Harbers.

2005. Parental care of the Blackish Tapaculo (*Scytalopus latrans*) in northeastern Ecuador. Ornitología Neotropical 16:283–286.

Hennessey, A. B., S. K. Herzog, and F. Sagot. 2003. Lista anotada de las Aves de Bolivia. Quinta Edición. Asociación Armonia/Birdlife International, Santa Cruz de la Sierra, Bolivia.

Hilty, S. L. and W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, USA.

Johnson, A. W. and J. D. Goodall. 1965. The birds of Chile and adjacent regions of Argentina, Bolivia, and Peru. Volume. 2. Platt Establecimientos Graficos S.A., Buenos Aires, Argentina.

Krabbe, N. and T. S. Schulenberg. 1997. Species limits and natural history of *Scytalopus* tapaculos (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. Ornithological Monographs 48:47–88.

Krabbe, N. and T. S. Schulenberg. 2003. Family Rhinocryptidae (tapaculos). Pages 748–787 *in* Handbook of the birds of the world. Volume 8. Broadbills to tapaculos (J. Del Hoyo, A. Elliot, and D. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Pulgarin-R, P. C. 2007. The nest and eggs of Spillmann's Tapaculo (*Scytalopus spillmanni*). Ornitología Colombiana 5:91–93.

Remsen Jr., J. V., A. Jaramillo, M. A. Nores, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, J. M. C. da Silva, D. F. Stotz, and K. J. Zimmer. 2008. A classification of the bird species of South America. American Ornithologists' Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.html.

Rosenberg, G. 1986. The nest of the Rusty-belted Tapaculo (*Liosceles thoracicus*). Condor 88:98.

Sick, H. 1993. Birds in Brazil: a natural history. Princeton University Press, Princeton, New Jersey, USA.

Skutch, A. 1972. Studies of tropical American birds. Publications of the Nuttall Ornithological Club Number 10.

Stiles, E. 1979. The nest and eggs of the White-browed Tapaculo (*Scytalopus superciliaris*). Condor 81:208.

Young, B. E. and W. Zuchowski. 2003. First description of the nest of the Silvery-fronted Tapaculo (*Scytalopus argentifrons*). Wilson Bulletin 115: 91–93.

Zimmer, J. T. 1939. Studies of Peruvian birds 32. The genus *Scytalopus*. American Museum Novitates. 1044:1–18.

Zimmer, K. J. and M. J. Isler. 2003. Family Thamnophilidae (typical antbirds). Pages 448–681 *in* Handbook of the birds of the world. Volume 8. Broadbills to tapaculos (J. Del Hoyo, A. Elliot, and D. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Zyskowski, K. and R. O. Prum. 1999. Phylogenetic analysis of the nest architecture of neotropical ovenbirds (Furnariidae). Auk 116:891–911.

The Wilson Journal of Ornithology 120(3):478–493, 2008

PHYLOGEOGRAPHIC PATTERNS OF DIFFERENTIATION IN THE ACORN WOODPECKER

MAGALI HONEY-ESCANDÓN,[1,4] BLANCA E. HERNÁNDEZ-BAÑOS,[1] ADOLFO G. NAVARRO-SIGÜENZA,[1] HESIQUIO BENÍTEZ-DÍAZ,[2] AND A. TOWNSEND PETERSON[3]

ABSTRACT.—Acorn Woodpecker (*Melanerpes formicivorus*) populations were sampled to evaluate geographic patterns of differentiation and connectivity across the species' range. We observed patterns of differentiation generally coincident with geographic patterns in plumage patterns with distinct subpopulations in Baja California Sur, northern Central America, southern Central America, and mainland Mexico north into the southwestern United States. We confirmed the existence of geographic genetic structuring of populations of this species, although shared haplotypes between Baja California Sur and mainland Mexico suggest that lineage sorting is not yet complete. The process of geographic differentiation and speciation is likely still underway in this group. *Received 31 January 2007. Accepted 26 October 2007.*

The montane forests of North and Central America have had a complex history and geography over the past 100,000 years (Graham 1975, Wells 1983). During the Pleistocene, montane areas, particularly in the northern part of the region, appear to have been largely covered by ice or tundra and, thus, uninhabitable for forest birds, whereas desert basins filled with what are presently 'montane' coniferous forests (Wells 1983). Pleistocene and Holocene climatic shifts must have had important implications for avian biogeography in terms of population connectivity and isolation, and likely affected the species inhabiting these biomes profoundly.

Studies have now addressed the climatic and biogeographic implications of Pleistocene-Holocene climate shifts (Hugall et al. 2002, Martínez-Meyer et al. 2004, Martínez-Meyer and Peterson 2006, Ruegg et al. 2006), but surprisingly few detailed phylogeographic studies of birds have been conducted to illustrate how climatic changes and habitat shifts influenced the evolution and differentiation of birds. Only *Aphelocoma* jays (Peterson 1992, Rice et al. 2003), *Sphyrapicus* sapsuckers (Cicero and Johnson 1995), MacGillivray's Warbler (*Oporornis tolmiei*) (Milá et al. 2000), and Hutton's Vireos (*Vireo huttoni*) (Cicero and Johnson 1992) have been studied in North American pine-oak (*Pinus-Quercus*) woodlands and forests. Patterns of genetic differentiation and the extent to which they do—or do not—relate to Pleistocene patterns of connection and disjunction of habitats are only beginning to be understood.

The objective of this paper is to present the results of molecular genetic studies of 98 individuals from 15 populations of Acorn Woodpeckers (*Melanerpes formicivorus*) across North and Central America. An earlier contribution based on many of the same samples as in this paper (Benítez-Díaz 1993) identified a series of morphologically distinct populations with major units including populations in California, Baja California Sur, mainland Mexico, Central America, and Colombia. Samples are lacking to represent the distinctive populations of northwestern South America, but sampling of the remainder of the distribution of the species is more or less intensive. This study, based on sequences of two mitochondrial genes, offers a first view of geographic patterns of genetic differentiation among populations of the Acorn Woodpecker.

METHODS

Samples and Sequencing.—Samples of muscle, heart, and liver collected from 98 individual Acorn Woodpeckers across most of the species' range (the distinct Colombian

[1] Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-399, México, D.F. 04510, México.

[2] Comisión Nacional para el Uso y Conocimiento de la Biodiversidad, Liga Periférico – Insurgentes Sur 4903, C.P. 14010, D.F. 14010, México.

[3] Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, KS 66045, USA.

[4] Corresponding author;
e-mail: behb@hp.fciencias.unam.mx

populations, and those of lowland areas in Belize and the remainder of the Petén region were not included for lack of access to samples; Fig. 1). We included sequences from 10 individuals of seven related species, including *Melanerpes lewis*, *M. aurifrons* (3 individuals), *M. uropygialis*, *M. pygmaeus* (2 individuals), *M. pucherani*, *Sphyrapicus nuchalis*, and (more distantly) *Coracias spatulatus* (Appendix). These samples were obtained from field collections by several of the authors; full specimen voucher specimens are deposited in the Museo de Zoología "Alfonso L. Herrera" of the Universidad Nacional Autónoma de México (UNAM), Field Museum of Natural History, and the University of Kansas Natural History Museum, supplemented by tissue samples associated with specimens kindly provided by the Barrick Museum of Natural History (University of Nevada–Las Vegas) and the Museum of Vertebrate Zoology (University of California–Berkeley). Data were obtained from GenBank for two outgroup individuals.

Total tissue DNA was extracted via DNEasy Extraction Kits (Qiagen, Valencia, CA, USA). Specific fragments were amplified via polymerase chain reaction (PCR) using primers spanning 334 bp of the mitochondrial gene ND2 segment (L5215 TAT CGG GCC CAT ACC CCG AAA AT; H5578 CCT TGA AGC ACT TCT GGG AAT CAG A) (Hackett 1996) and a 608 bp fragment of the cytochrome *b* gene (L15413 CTG ACA AAA TTC CAT TTC ACC C; H16064 CTT CAG TTT TTG GTT TAC AAG ACC) (Kocher et al. 1989 and Sorenson et al. 1999, respectively). All numbers refer to the 3-prime end of the primer reference of the complete mtDNA sequence of the domestic chicken (*Gallus gallus*) (Desjardins and Morais 1990).

A typical ND2 amplification involved 35 cycles of 95° C for 1 min, 48° C for 2 min, 72° C for 3 min, and a final 10 min extension period at 72° C. Cyt*b* amplification involved 27 cycles of 94° C for 1 min, 50° C for 1 min, and 72° C for 2 min, followed by a 7 min extension period at 72° C. PCRs were conducted on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA). Products were verified on a 1% agarose gel with added ethidium bromide and cleaned using a QiaQuick Kit (Qiagen, Valencia, CA, USA), obtaining a final volume of 15–30 μL of PCR products.

We purified PCR products using Geneclean® (Qbiogene, Bio101® Systems, Krackeler Scientific Inc., Albany, NY, USA) and Millipore purification kits following manufacturers' protocols. Purified PCR products were sequenced on a Perkin-Elmer ABI 373 automatic sequencing machine. Sequences were cleaned using Chromas 1.45 (McCarthy 1996), and aligned using ClustalX (Thompson et al. 1997). We corroborated the origin of our sequences by combining at least two of the following: amplifying overlapping gene segments, sequencing both DNA strands, and/or using multiple individuals of single populations.

Statistical Analyses.—We used MEGA 2.0 (Kumar et al. 2004) to derive basic statistics regarding sequences, and their variation and diversity. We used Arlequin (Schneider et al. 2000) to calculate Nei's pairwise differences (raw distances corrected following Nei [1987]) among populations, as well as F_{st} values. DnaSP Version 4.10 (Rozas et al. 2003) was used to calculate nucleotide diversity (π) and haplotype diversity (κ). We used TCS Version 1.13 (Clement et al. 2000) to estimate networks summarizing mutational differences among haplotypes. We compared matrices of Nei's corrected genetic distances with matrices of straight-line geographic distances separating populations using a Mantel test; we plotted the ratio of genetic to geographic distances on maps to visualize spatial patterns of genetic differentiation on a per kilometer basis.

Only informative characters and unique haplotypes were used for parsimony searches using *Coracias* as the only designated outgroup to avoid problems of non-monophyly of in-group taxa. Maximum parsimony trees were constructed for ND2 and cyt*b* sequences both separately and combined, using heuristic search options in PAUP 4.0 (Swofford 1999) with TBR and ACCTRAN optimization options. We used character-based bootstrap analysis (100 replicates) to estimate support for each node in the resulting tree.

ModelTest 3.0 (Posada and Crandall 1998) was used to identify appropriate models of sequence evolution for haplotypes of *Melanerpes formicivorus*. Bayesian inference (BI) ap-

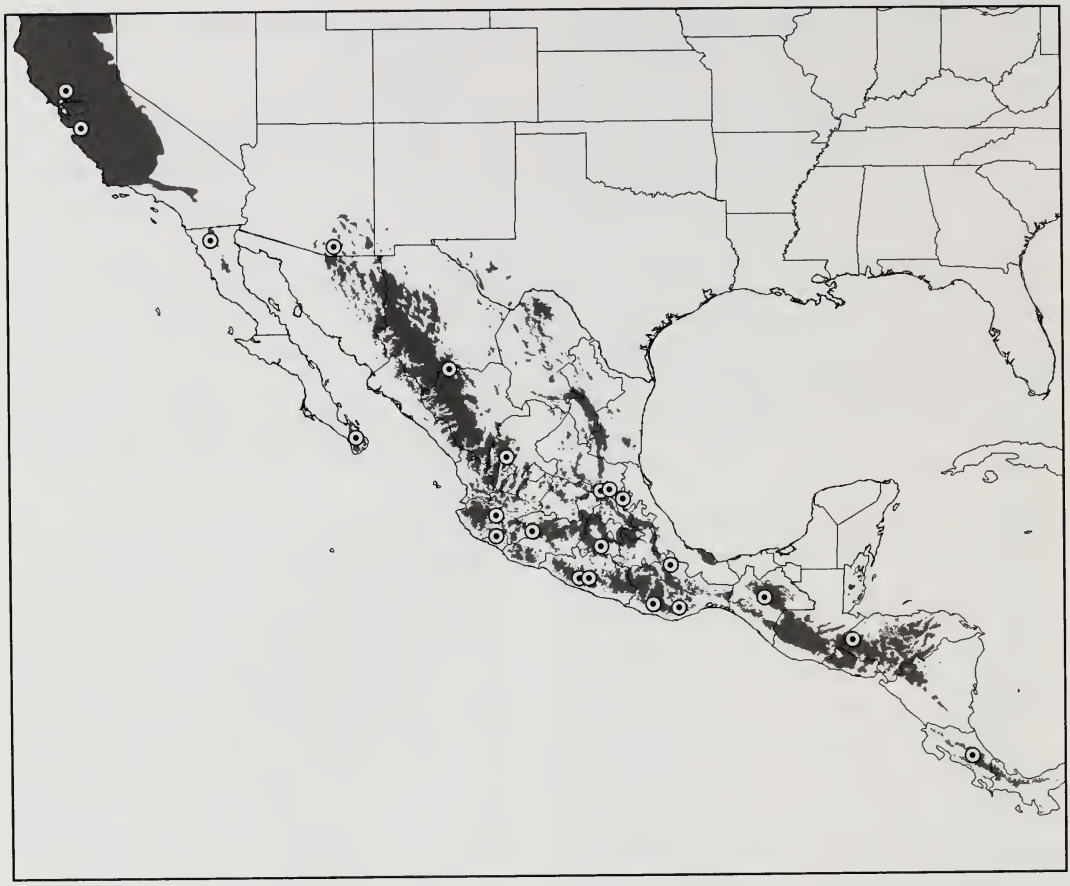


FIG. 1. Geographic distribution of *Melanerpes formicivorus* (shaded) showing localities where samples were obtained.

proaches, as implemented in Mr.Bayes Version 3.1 (Huelsenbeck and Ronquist 2001) used the substitution model GTR (nset = 6) for the number of rate parameters and a gamma distribution for rates at each site. We ran four Markov Chains (random starting trees) for 10^7 generations, each sampling every 250 generations and identifying stationarity visually. We allowed an initial "burn-in" of 250 trees to avoid non-optimal solutions and computed a majority-rule consensus tree, as well as posterior probabilities for each node (Huelsenbeck et al. 2002).

RESULTS

Genetic Variation.—We obtained a total of 942 base pairs across the two genes. Of these sites, 586 were conserved, 356 were variable, and 231 were parsimony-informative. The transition/transversion ratio was 3.4 and nucleotide composition was T = 0.26, C = 0.36, A = 0.27, and G = 0.11. Nucleotide diversity was 0.00482 and haplotype diversity was 0.851 with lowest nucleotide diversity values in Baja California Norte and Oaxaca populations. Overall, we found 44 haplotypes (Fig. 2) among the 98 sequences that were distinguishable by 66 polymorphic sites. Almost all (41) haplotypes were restricted to single populations. Haplotype H4 was present in single individuals from population samples from Guerrero and Hidalgo, Mexico; haplotype H35 occurred in seven individuals from Baja California Norte, Mexico, and California, USA, and (most impressively) H29 was found in 33 individuals from 10 localities from Arizona south to Honduras.

Pairwise average population differences (Table 1) ranged from 0 to 8.07 within the Arizona sample, and 0 to 8.35 in the Baja Cal-

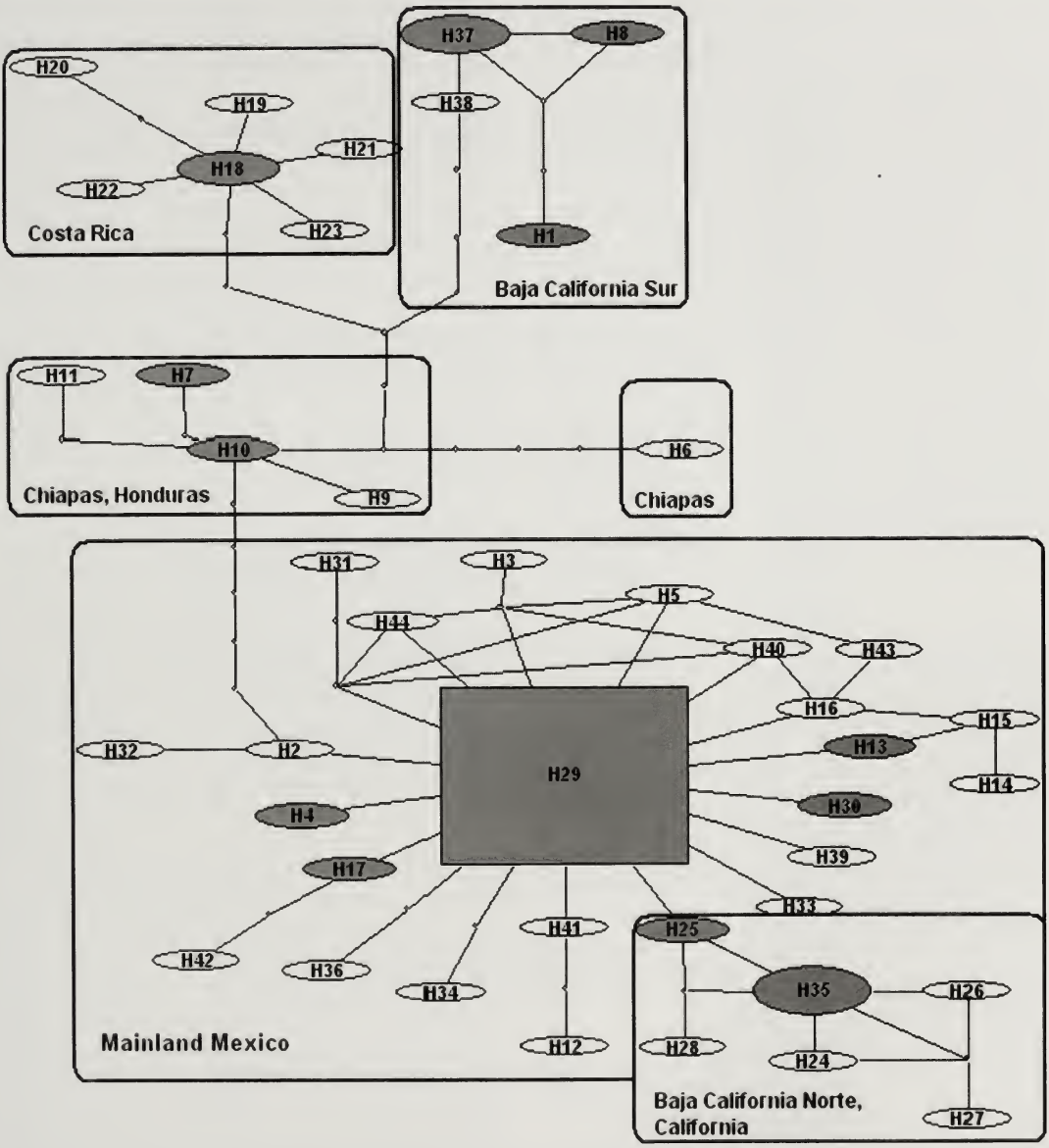


FIG. 2. Haplotype network of the 44 haplotypes of *Melanerpes formicivorus*. Mutational steps are indicated by the number of line segments connecting haplotypes. The size of the ovals represents the number of samples with that haplotype; shaded ovals are haplotypes with more than one sample.

ifornia Norte versus Baja California Sur, Mexico samples. The overall F_{st} statistic for the species was 0.484. Pairwise values between population samples ranged from 0 (several population pairs) to >0.7, most related to the Baja California Sur and Baja California Norte populations and, to a lesser extent, with the Central American populations.

The haplotype network (Fig. 2) had several features. One haplotype (H29) was common, occurring in about one-third of all individuals. Closely associated to this haplotype were 22 other haplotypes that differed by ≤3 mutations from H29; overall, this group of haplotypes generally corresponds to populations of mainland Mexico and Arizona (with one representative from as far south as Honduras). Closely associated to the mainland Mexico

TABLE 1. Pairwise average differences (below the diagonal) and pairwise F_{st} values (above the diagonal) for each population analyzed. Significant values are in italics and the cells along the diagonal show the average pairwise differences within each population. The population of QRO was grouped with HGO to avoid biased results, as it consisted of only one sample. Negative F_{st} values are considered equivalent to zero.

	DGO	GRO	HGO	JAL	MICH	OAX	ZAC	ARI	BCS	HON	CHIS	CR	CAL	BCN
DGO	***0.8585***	−0.0031	0.0113	*0.1835*	0.0072	−0.0110	0.0185	0.2239	*0.7603*	*0.6602*	*0.8047*	*0.8424*	*0.4987*	*0.6242*
GRO	0.0001	***0.6675***	−0.0608	*0.1819*	−0.0046	0.0001	−0.0272	0.1741	*0.7487*	*0.6406*	*0.7966*	*0.8407*	*0.5124*	*0.6993*
HGO	0.0001	−0.0371	***0.4450***	*0.2273*	−0.0007	−0.0082	0.0312	*0.3197*	*0.7893*	*0.7278*	*0.8543*	*0.8717*	*0.5628*	*0.7494*
JAL	*0.2784*	*0.2784*	*0.2782*	***1.4469***	0.0695	0.1938	*0.1835*	*0.2816*	*0.7390*	*0.6510*	*0.7874*	*0.8200*	*0.4724*	*0.5267*
MICH	0.0179	0.0178	−0.0102	0.1154	***1.7179***	−0.0119	0.0320	0.1762	*0.7411*	*0.6043*	*0.7580*	*0.8006*	*0.4172*	*0.4286*
OAX	0.0001	0.0001	*0.0001*	0.2781	0.0179	***0.3337***	−0.0007	0.2238	*0.7653*	*0.6830*	*0.8258*	*0.8636*	*0.5464*	*0.8254*
ZAC	0.0279	−0.0093	0.0278	*0.3065*	0.0459	0.0277	***1.2805***	0.2106	*0.7447*	*0.6396*	*0.7882*	*0.8175*	*0.4599*	*0.5005*
ARI	−0.0050	−0.1184	−0.0061	0.2768	−0.0657	−0.0034	−0.1260	***8.0693***	*0.5824*	*0.0345*	*0.2889*	*0.6094*	*0.4159*	*0.3032*
BCS	*7.3404*	*7.0305*	*7.3378*	*6.8020*	*7.3656*	*7.3367*	*6.7947*	*4.8973*	***3.1555***	*0.6182*	*0.6772*	*0.7196*	*0.7813*	*0.7691*
HON	*3.5340*	*3.2796*	*3.5324*	*3.8177*	*3.5244*	*3.5317*	*3.3949*	0.0000	*5.3618*	***4.0302***	0.1108	*0.6413*	*0.7105*	*0.6927*
CHIS	*7.0862*	*6.7454*	*7.0834*	*7.3741*	*7.1119*	*7.0823*	*6.8917*	*2.5947*	*6.9574*	0.5021	***4.7028***	*0.7311*	*0.8217*	*0.8159*
CR	*6.0534*	*5.7148*	*6.0515*	*6.3384*	*6.0767*	*6.0507*	*5.8588*	*3.3625*	*6.0424*	*3.4981*	*5.0522*	***1.3361***	*0.8504*	*0.8775*
CAL	*1.0028*	*1.0027*	*1.0024*	*1.1458*	*0.9942*	*1.0027*	*1.0188*	*0.9327*	*8.0524*	*4.4636*	*7.9960*	*6.9576*	***1.1127***	−0.1166
BCN	*1.0018*	*1.0018*	*1.0016*	*1.2807*	*1.0201*	*1.0015*	*1.0299*	*1.0011*	*8.3542*	*4.5430*	*8.1008*	*7.0641*	−0.0002	***0.0000***

haplotype assemblage are six haplotypes restricted to Baja California Norte and California. Less closely associated with the main haplotype mass, however, are four haplotypes from Chiapas and northern Central America (7 mutational steps from H29, one sample an additional 6 steps distant) and one from Arizona (H11). More removed from H29 are clusters corresponding to Baja California Sur individuals (4 haplotypes, 14 mutational steps from H29) and Costa Rican individuals (6 individuals, 13 mutational steps from H29). One Baja California Sur haplotype (H36) grouped with the mainland Mexico assemblage of haplotypes, two mutational steps from H29, the most common haplotype.

A generally positive relationship was observed in plots of genetic distances versus geographic distances. The relationship is not tight (Fig. 3), but is statistically significant (Mantel's test, observed $r = 0.792$, $P < 0.001$). The impressive genetic disconnection of the Baja California Sur populations can be appreciated by standardizing genetic distances to geographic distances and plotting these indices of differentiation per kilometer on maps (Fig. 3). Central American populations are also disconnected from northern populations genetically.

Phylogenetic Patterns.—The MP analysis yielded ≥500 equally parsimonious 532-step trees (CI = 0.594, RI = 0.812; Fig. 4). These trees grouped all *Melanerpes formicivorus* populations as a monophyletic group with high bootstrap support (100% of bootstrap replicates). Subclades corresponding to individuals from Baja California Sur (84% support), northern Central America (Chiapas, Honduras; 80% support), and southern Central America (Costa Rica; 73% support) were found within this clade, although none had solid branch support in the bootstrap analyses. The remaining individuals in the study were grouped in one large, but poorly supported clade (51% bootstrap support) of individuals from mainland Mexico, Arizona, California, and Baja California Norte. Two individuals (from Guerrero and Zacatecas) were not connected with any of the subclades within the species, one Baja California Sur individual (haplotype H36) grouped with the mainland Mexico assemblage, and one Arizona individual (haplotype H11) grouped with the Chiapas-Honduras clade.

The BI analyses were based on the TVM + I + G model of substitution and showed a topology (Fig. 5) generally close to that of the MP tree. The clade corresponding to all *Melanerpes formicivorus* populations was well-defined and subclades with intriguing but inconclusive constitution were encountered. In particular, we recovered the Baja California Sur (0.97 posterior probability), northern Central America with the single Arizona sample (0.99 posterior probability), and southern Central America (0.78 posterior probability) nodes. We encountered a weakly supported node corresponding to the California and Baja California Norte samples (0.63 posterior probability); the mainland Mexico and Arizona and single Baja California Sur samples formed a large and poorly-defined assemblage.

DISCUSSION

An earlier morphological analysis (Benítez-Díaz 1993), in many cases of precisely the same individuals as were analyzed in this study, found marked subdivision of the species into seven groups, two of which (Belize and Colombia) were not analyzed in this study. These groups were supported by the distribution of genetic variation found in our study, albeit not strongly or with marked genetic differentiation. Recalculating F_{st} statistics hierarchically, we found that 73.7% of overall genetic variation was assorted among these five groups, as opposed to 26% within them, suggesting these groups have explanatory power regarding population differentiation in the overall complex.

The five groups included in this study, with one exception, were distinct from one another in terms of mutational steps in a haplotype network. The exception was that of the California/Baja California Norte populations, which, although they grouped together, were only one mutational step from the mainland Mexico haplotype group. Other groups were more distinct; each was ≥6 mutational steps removed from all other groups. Thus, the haplotypes of the plumage-based groups appear to differ markedly from group to group. Given the high number of unique haplotypes, additional sampling may prove necessary for the details of the situation to be completely clear.

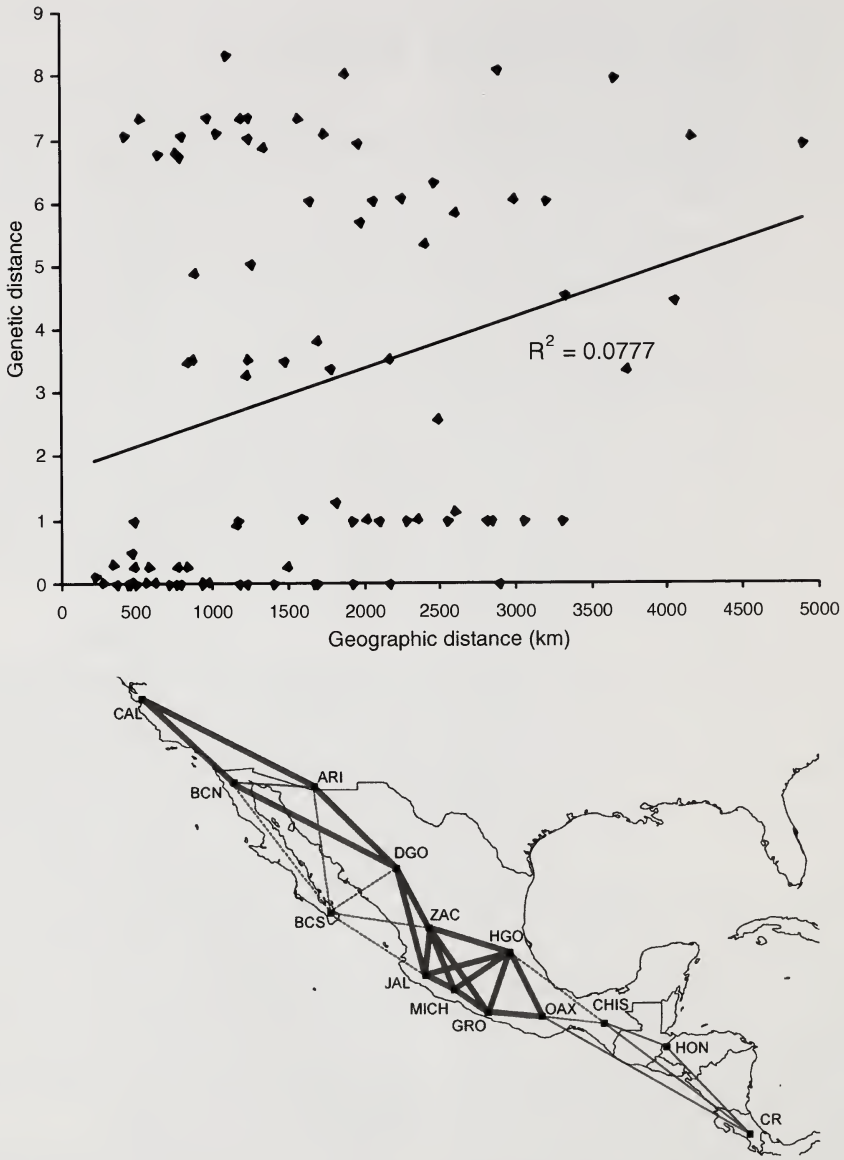


FIG. 3. Geographic patterns of genetic differentiation: (top) relationship between genetic distance and geographic distance based on 15 collecting localities; (bottom) map of genetic distance/km illustrating patterns of genetic connectivity among Acorn Woodpecker population samples. Thick continuous lines indicate rates of <1 genetic distance unit/km, thin continuous lines indicate rates of 1–5 genetic distance unit/km, and thin broken lines indicate rates of >5 genetic distance unit/km.

Our results clearly indicate lack of full establishment of reciprocal monophyly among the various populations in spite of the overall picture of differentiation. This muted differentiation is visible in both the relatively unresolved and poorly supported trees that were recovered, and in the mixture of one Baja California Sur haplotype among the "mainland Mexico" haplotypes and the presence of one (H29, the most common haplotype) in Honduras in both the phylogenetic analyses and the haplotype network.

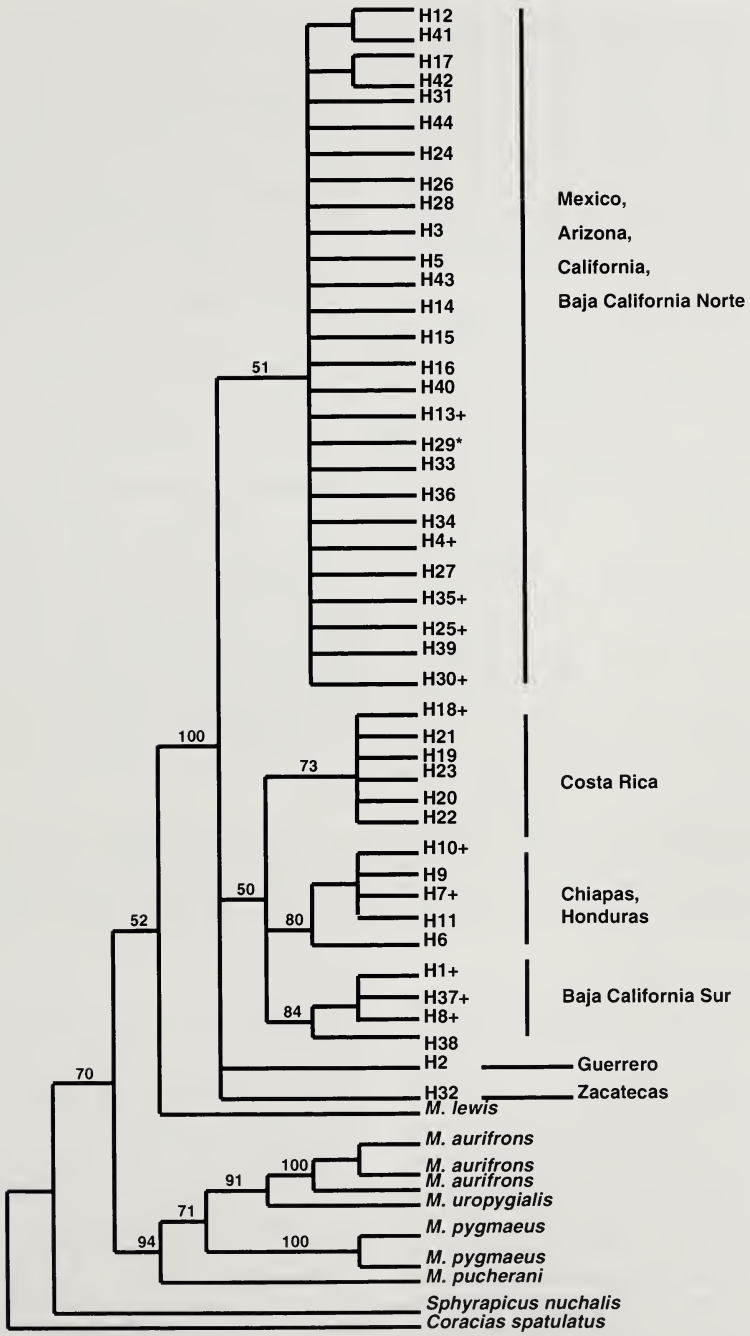


FIG. 4. Maximum parsimony tree (50% majority rule consensus) of the 44 haplotypes of Acorn Woodpeckers and 10 outgroup samples. Numbers on branches indicate bootstrap support. + = haplotypes with more than one sample; * = the most common haplotype (which was represented in a single sample from Honduras). Note that some branches have relatively low bootstrap support and may not be robust hypotheses of relationships.

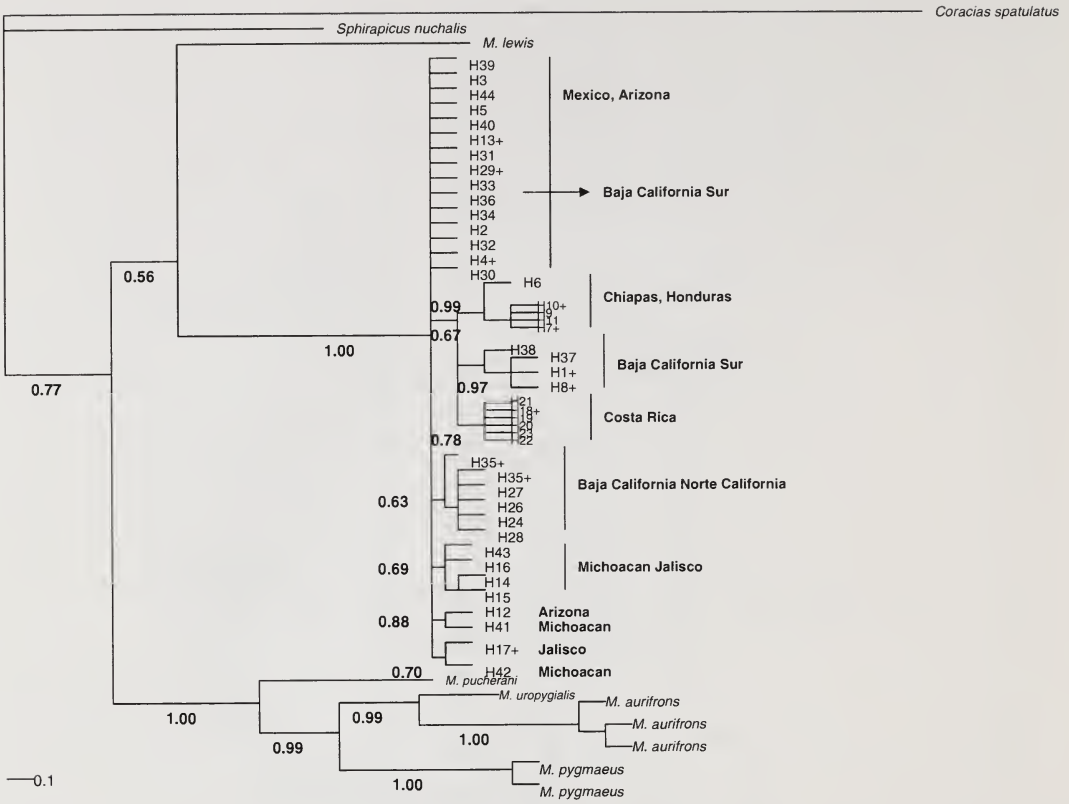


FIG. 5. Bayesian inference tree of the 44 haplotypes and 10 outgroups. Numbers below the branches show the values of the posterior probability of each branch. + = haplotypes with more than one sample; * = the most common haplotype (which was represented in a single sample from Honduras). Note that some of the branches have relatively low probabilities associated and may not be robust hypotheses of relationships.

Benítez-Díaz (1993) documented the existence of seven subgroups within *Melanerpes formicivorus* on the basis of external phenotype. These groups should be considered for formal taxonomic recognition (Navarro and Peterson 2004), at least under the Evolutionary Species Concept (Wiley 1978) and the Phylogenetic Species Concept (Zink and McKitrick 1995, Zink 1996). Benítez-Díaz (1993) recommended recognition of *Melanerpes bairdi* of California and Baja California Norte, *M. angustifrons* of Baja California Sur, *M. formicivorus* of the southwestern United States and mainland Mexico, *M. lineatus* of northern Central America, *M. striatipectus* of southern Central America, *M. albeolus* of Belize, and *M. flavigula* of Colombia. *M. albeolus* and *M. flavigula* were not available to us for molecular analysis and we did not find marked differentiation between populations in California and Mexico. Hence, we focus attention on *M. formicivorus* (including California populations of the *bairdi* group), *M. angustifrons*, *M. lineatus*, and *M. striatipectus* in the rest of our discussion.

Benítez-Díaz's (1993) general picture of differentiation of Acorn Woodpecker populations was supported, but decisions regarding species limits were less clear. From the perspective of the Biological Species Concept (AOU 1998), these populations can be interpreted either as (1) exchanging few genes after a relatively recent separation, or (2) still exchanging genes (which may cause the intermixing of haplotypes), which would probably point to caution in splitting populations under this concept. The Phylogenetic Species Concept would clearly recognize these different forms as species in view of their distinctiveness in plumage, but would hold back from recognition using molecular

characters on the basis of intermixing of haplotypes from Baja California Sur, mainland Mexico, and Central America. Finally, under the Evolutionary Species Concept, one would most likely accord them species status, given that not only are populations apparently in the process of diverging, but unique phenotypic characters are now fixed in at least some populations.

The patterns of genetic variation and differentiation identified would appear to correspond closely to known Pleistocene geography of pine-oak woodlands at the Last Glacial Maximum (LGM, ca. 20,000 years ago). That is, at LGM, montane woodlands moved on large spatial scales, broadly invading the southwestern North American deserts (Lanner and Van Devender 1981, Spaulding et al. 1983, Wells 1983). The major zones of genetic differentiation in *Melanerpes formicivorus* are between the southern tip of Baja California and the California/Mexico portion of the range, and across the Isthmus of Tehuantepec—the lack of differentiation across the Mohave Desert may reflect the Pleistocene connectivity of populations of this species.

ACKNOWLEDGMENTS

We thank our companions (particularly Noé Vargas-Barajas, Scott Baker, Patricia Escalante, and Laura and Fernando Villaseñor-Gómez, among many others) for invaluable assistance and support during field collections. Colleagues at the Museum of Vertebrate Zoology and the Barrick Museum of Natural History kindly provided samples to add to our set of specimens; Eduardo Morales (Instituto de Historia Natural y Ecología) kindly provided samples from Chiapas. Funding was provided by the National Geographic Society and the U.S. National Science Foundation. The laboratory research was supported by DGAPA IN-208700 and IN-211407, SEMARNAT-CONACYT Sectorial Fund C01-0265, and a CONACYT scholarship to MHE. We thank Gabriela García-Deras, Nandadevi Cortés-Rodríguez, and Laura Márquez Valdelamar for technical support.

LITERATURE CITED

American Ornithologists Union (AOU). 1998. Check-list of North American birds. Seventh Edition. American Ornithologists' Union, Washington, D.C., USA.

Benítez-Díaz, H. 1993. Geographic variation in coloration and morphology of the Acorn Woodpecker. Condor 95:63–71.

Cicero, C. A. and N. K. Johnson. 1992. Genetic differentiation between populations of Hutton's Vireo (Aves: Vireonidae) in disjunct allopatry. Southwestern Naturalist 37:344–348.

Cicero, C. and N. K. Johnson. 1995. Speciation in sapsuckers (*Sphyrapicus*). III. Mitochondrial-DNA sequence divergence at the cytochrome-b locus. Auk 112:147–163.

Clement, M., D. Posada, and K. A. Crandall. 2000. TCS: a computer program to estimate gene genealogies. Molecular Ecology 9:1657–1659.

Desjardins, P. and R. Morais. 1990. Sequence and gene organization of the chicken mitochondrial genome. Journal of Molecular Biology 212:599–634.

Graham, A. 1975. Late Cenozoic evolution of tropical lowland vegetation in Veracruz, Mexico. Evolution 29:723–735.

Hackett, S. J. 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). Molecular Phylogenetics and Evolution 5: 368–382.

Huelsenbeck, J. P. and F. Ronquist. 2001. MRBAYES: bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

Huelsenbeck, J. P., B. Larget, R. E. Miller, and F. Ronquist. 2002. Potential applications and pitfalls of Bayesian inference of phylogeny. Systematic Biology 51:673–688.

Hugall, A., C. Moritz, A. Moussalli, and J. Stanisic. 2002. Reconciling paleodistribution models and comparative phylogeography in the wet tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). Proceedings of the National Academy of Sciences USA 99:6112–6117.

Kocher, T. D., W. K. Thomas, A. Meyer, S. V. Edwards, S. Pääbo, F. X. Villablanca, and A. C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences USA 86:6196–6200.

Kumar, S., K. Tamura, and M. Nei. 2004. MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. Briefings in Bioinformatics 5:150–163.

Lanner, R. M. and T. R. Van Devender. 1981. Late Pleistocene pinon pines in the Chihuahuan Desert. Quaternary Biology 15:278–290.

Martínez-Meyer, E. and A. T. Peterson. 2006. Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-recent transition. Journal of Biogeography 33:1779–1789.

Martínez-Meyer, E., A. T. Peterson, and W. W. Hargrove. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13:305–314.

McCarthy, C. 1996. Chromas 1.45. Griffith University, Southport, Queensland, Australia.

Milá, B., D. J. Girman, M. Kimura, and T. B. Smith.

2000. Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. Proceedings of the Royal Society of London Series B 267: 1033–1040.

Navarro, A. G. and A. T. Peterson. 2004. An alternative species taxonomy of the birds of Mexico. Biota Neotropica 4 (2). http://www.biotaneotropica.org.br/v4n2/pt/abstract?taxonomic-review+BN03504022004.

Nei, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York, USA.

Peterson, A. T. 1992. Phylogeny and rates of molecular evolution in the jays of the genus *Aphelocoma* (Corvidae). Auk 109:134–148.

Posada, D. and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.

Rice, N. H., E. Martínez-Meyer, and A. T. Peterson. 2003. Ecological niche differentiation in the *Aphelocoma* jays: a phylogenetic perspective. Biological Journal of the Linnaean Society 80:369–383.

Rozas, J. J., C. Sánchez-DelBarrio, X. Messeguer, and R. Rozas. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19:2496–2497.

Ruegg, K. C., R. J. Hijmans, and C. Moritz. 2006. Climate change and the origin of migratory pathways in the Swainson's Thrush, *Catharus ustulatus*. Journal of Biogeography 33:1172–1182.

Schneider, S., D. Roessle, and L. Excoffier. 2000. Arlequin Version 2.000: a software for population genetics data analysis. University of Geneva, Geneva, Switzerland.

Sorenson, M. D., J. C. Ast, D. E. Dimcheff, T. Yuri, and D. P. Mindell. 1999. Primers for a PCR-based approach to mitochondrial genome sequencing birds and other vertebrates. Molecular Phylogenetics and Evolution 12:105–114.

Spaulding, W. G., E. B. Leopold, and T. R. Van Devender. 1983. Late Wisconsin paleoecology of the American Southwest. Pages 259–293 *in* Late Quaternary environments of the United States. The late Pleistocene (S. C. Porter, Editor). Volume 1. University of Minnesota Press, Minneapolis, USA.

Swofford, D. L. 1999. PAUP* Phylogenetic analysis using parsimony. Version 4.0. Sinauer Associates, Sunderland, Massachusetts, USA.

Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jeanmougin, and D. J. Higgins. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 24:4876–4882.

Wells, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs 53:341–382.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Systematic Zoology 27:17–26.

Zink, R. M. 1996. Species concepts, speciation and sexual selection. Journal of Avian Biology 27:1–6.

Zink, R. M. and M. C. McKitrick. 1995. The debate about species concepts and its implications for ornithology. Auk 112:701–719.

APPENDIX. Data for each of the samples used in this study. Haplotype number shows the corresponding haplotype to the sample sequence (Fig. 2).

Standard ID	Museum/catalog number	Haplotype number	Field catalog number	Country	State	Specific locality
ARI –1		H11	DHB3438	USA	Arizona	Santa Rita Mountains, Garner Canyon
ARI–2		H29	DHB3588	USA	Arizona	Santa Rita Mountains, Temporal Gulch
ARI–3		H12	DHB3570	USA	Arizona	Santa Rita Mountains, Garner Canyon
BCN–1	FMNH 356616	H35	MXJ274	Mexico	Baja California Norte	La Rosa de Castilla, 4 km N
BCN–2	FMNH 393841	H35	MXJ270	Mexico	Baja California Norte	La Rosa de Castilla, 4 km N
BCN–3	FMNH 393842	H35	MXJ272	Mexico	Baja California Norte	La Rosa de Castilla, 4 km N
BCN–4	FMNH 395782	H35	MXJ271	Mexico	Baja California Norte	La Rosa de Castilla, 4 km N
BCS–1	FMNH 356617	H37	MXJ313	Mexico	Baja California Sur	La Burrera, 6 km N, 18 km E Todos Santos, Sierra de la Laguna
BCS–2	FMNH 356618	H38	MXJ314	Mexico	Baja California Sur	La Burrera, 6 km N, 18 km E Todos Santos, Sierra de la Laguna
BCS–3	FMNH 356619	H1	MXJ318	Mexico	Baja California Sur	La Burrera, 6 km N, 18 km E Todos Santos, Sierra de la Laguna
BCS–4	FMNH 395783	H36	MXJ312	Mexico	Baja California Sur	La Burrera, 6 km N, 18 km E Todos Santos, Sierra de la Laguna
BCS–5	FMNH 395784	H37	MXJ315	Mexico	Baja California Sur	La Burrera, 6 km N, 18 km E Todos Santos, Sierra de la Laguna
BCS–6	FMNH 395785	H37	MXJ316	Mexico	Baja California Sur	La Burrera, 6 km N, 18 km E Todos Santos, Sierra de la Laguna
BCS–7	FMNH 395787	H37	MXJ319	Mexico	Baja California Sur	La Burrera, 6 km N, 18 km E Todos Santos, Sierra de la Laguna
BCS–8	FMNH 395788	H37	MXJ320	Mexico	Baja California Sur	La Burrera, 6 km N, 18 km E Todos Santos, Sierra de la Laguna
BCS–9		H8	CONACYT708A	Mexico	Baja California Sur	Rancho San Dionisio
BCS–10		H8	CONACYT708B	Mexico	Baja California Sur	Rancho San Dionisio
BCS–11		H1	B4481	Mexico	Baja California Sur	Rancho San Dionisio
CAL–1	MVZ179855	H28		USA	California	4 km E of Jamesburg, Hastings Natural History Reservation

APPENDIX. Continued.

Standard ID	Museum/catalog number	Haplotype number	Field catalog number	Country	State	Specific locality
CAL–2	MVZ179821	H26		USA	California	4 km E of Jamesburg, Hastings Natural History Reservation
CAL–3	MVZ179853	H25		USA	California	4 km E of Jamesburg, Hastings Natural History Reservation
CAL–4	MVZ179857	H35		USA	California	4 km E of Jamesburg, Hastings Natural History Reservation
CAL–5	MVZ178440	H25		USA	California	4 km E of Jamesburg, Hastings Natural History Reservation
CAL–6	MVZ179852	H27		USA	California	Jamesburg
CAL–7	MVZ178120	H24		USA	California	Hwy. 12 at Oakmont, Santa Rosa
CAL–8	MVZ179856	H35		USA	California	ca. mile marker 18, Carmel Valley Rd.
CAL–9	MVZ179854	H35		USA	California	0.8 km N and 1.6 km W Red Rock
CHIS–1	IHNE1	H6	CHIS03	Mexico	Chiapas	San Cristóbal de las Casas
CHIS–2	IHNE2	H7	CHIS06	Mexico	Chiapas	San Cristóbal de las Casas
CHIS–3	IHNE3	H7	CHIS08	Mexico	Chiapas	San Cristóbal de las Casas
CR–1	FMNH 394306	H18	HBD14	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte
CR–2	FMNH 394308	H19	HBD16	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte
CR–3	FMNH 394309	H20	HBD17	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte
CR–4	FMNH 394310	H21	HBD18	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte
CR–5	FMNH 394311	H22	HBD19	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte
CR–6	FMNH 394312	H23	HBD20	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte
CR–7	FMNH 394313	H18	HBD21	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte
CR–8	FMNH 394314	H18	HBD22	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte
CR–9	FMNH 394315	H18	HBD23	Costa Rica	San Jose	Villa Mills, Cerro de la Muerte

APPENDIX. Continued.

Standard ID	Museum/catalog number	Haplotype number	Field catalog number	Country	State	Specific locality
DGO–1	FMNH 356609	H29	MXJ207	Mexico	Durango	Villa Ocampo, 3 km N, 2 km E
DGO–2	FMNH 356614	H34	MXJ231	Mexico	Durango	Villa Ocampo, 3 km N, 2 km E
DGO–3	FMNH 393836	H29	MXJ205	Mexico	Durango	Villa Ocampo, 3 km N, 2 km E
DGO–4	FMNH 393838	H33	MXJ227	Mexico	Durango	Villa Ocampo, 3 km N, 2 km E
DGO–5	FMNH 393839	H29	MXJ228	Mexico	Durango	Villa Ocampo, 3 km N, 2 km E
DGO–6	FMNH 395776	H29	MXJ208	Mexico	Durango	Villa Ocampo, 3 km N, 2 km E
DGO–7	FMNH 395777	H29	MXJ213	Mexico	Durango	Villa Ocampo, 3 km N, 2 km E
GRO–1	FMNH 356624	H4	MXJ469	Mexico	Guerrero	Toro Muerto, Sierra de Atoyac
GRO–2	FMNH 356626	H29	MXJ475	Mexico	Guerrero	Nueva Delhi, Sierra de Atoyac
GRO–3	FMNH 393849	H29	MXJ472	Mexico	Guerrero	Nueva Delhi, Sierra de Atoyac
GRO–4	FMNH 394194	H2	BMM049	Mexico	Guerrero	El Falsanal
GRO–5	FMNH 394195	H29	BMM050	Mexico	Guerrero	El Falsanal
GRO–6	FMNH 395792	H29	MXJ470	Mexico	Guerrero	Toro Muerto, Sierra de Atoyac
HGO–1	FMNH 394196	H3	BMM103	Mexico	Hidalgo	Tlanchinol, 5 km E
HGO–2	FMNH 394197	H29	BMM104	Mexico	Hidalgo	Tlanchinol, 5 km E
HGO–3	FMNH 394199	H29	BMM106	Mexico	Hidalgo	Tlanchinol, 5 km E
HGO–4	FMNH 394201	H4	BMM109	Mexico	Hidalgo	Tlanchinol, 5 km E
HGO–5	FMNH 394204	H29	BMM392	Mexico	Hidalgo	Tlanchinol, 5 km E
HGO–6	FMNH 394205	H5	BMM393	Mexico	Hidalgo	Tlanchinol, 5 km E
HGO–7	FMNH 394208	H29	BMM396	Mexico	Hidalgo	Tlanchinol, 5 km E
HGO–8		H29	HGSL23	Mexico	Hidalgo	Cerro Jarros, 1 km E El Sótano
HGO–9	FMNH 394317	H29	MXJ060	Mexico	Hidalgo	Jacala, 4 km N, 2 km E
HON–1		H10	DHB2893	Honduras	Copán	Ruinas de Copán, 10 km ENE
HON–2		H9	DHB2890	Honduras	Copán	Ruinas de Copán, 15 km ENE

APPENDIX. Continued.

Standard ID	Museum/catalog number	Haplotype number	Field catalog number	Country	State	Specific locality
HON–3		H10	DB3169	Honduras	Copán	Ruinas de Copán, 15 km ENE
HON–4		H29	DB3576	Honduras	Copán	Ruinas de Copán, 15 km ENE
JAL–1	FMNH 394297	H13	HBD02	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
JAL–2	FMNH 394298	H13	HBD04	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
JAL–3	FMNH 394299	H14	HBD05	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
JAL–4	FMNH 394300	H16	HBD07	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
JAL–5	FMNH 394302	H17	HBD09	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
JAL–6	FMNH 394303	H17	HBD10	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
JAL–7	FMNH 395807	H29	HBD01	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
JAL–8	FMNH 395808	H29	HBD03	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
JAL–9	FMNH 395809	H15	HBD06	Mexico	Jalisco	Las Joyas, Sierra de Manantlan
MICH–1	FMNH 356620	H41	MXJ345	Mexico	Michoacan	Periban, 5 km S, Cerro de Tancitaro
MICH–2	FMNH 356621	H42	MXJ346	Mexico	Michoacan	Periban, 5 km S, Cerro de Tancitaro
MICH–3	FMNH 356622	H43	MXJ348	Mexico	Michoacan	Periban, 5 km S, Cerro de Tancitaro
MICH–4	FMNH 356623	H29	MXJ350	Mexico	Michoacan	Periban, 5 km S, Cerro de Tancitaro
MICH–5	FMNH 395789	H29	MXJ347	Mexico	Michoacan	Periban, 5 km S, Cerro de Tancitaro
MICH–6	FMNH 393844	H39	MXJ340	Mexico	Michoacan	Periban, 5 km S, Cerro de Tancitaro
MICH–7	FMNH 393845	H40	MXJ341	Mexico	Michoacan	Periban, 5 km S, Cerro de Tancitaro
MICH–8	FMNH 393847	H29	MXJ343	Mexico	Michoacan	Periban, 5 km S, Cerro de Tancitaro
OAX–1	FMNH 356627	H29	MXJ604	Mexico	Oaxaca	El Zacatal

APPENDIX. Continued.

Standard ID	Museum/catalog number	Haplotype number	Field catalog number	Country	State	Specific locality
OAX–2	FMNH 393850	H29	MXJ602	Mexico	Oaxaca	El Zacatal
OAX–3	FMNH 393851	H29	MXJ603	Mexico	Oaxaca	El Zacatal
OAX–4	FMNH 393853	H29	MXJ611	Mexico	Oaxaca	El Zacatal
OAX–5	FMNH 395795	H44	MXJ608	Mexico	Oaxaca	El Zacatal
OAX–6	FMNH 394192	H29	BMM319	Mexico	Oaxaca	Santa Rosa, 2 km S
QRO–1		H29	QRO104	Mexico	Queretaro	Santa Inés, 2 km W
ZAC–1	FMNH 356603	H30	MXJ172	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
ZAC–2	FMNH 356604	H31	MXJ173	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
ZAC–3	FMNH 356605	H32	MXJ187	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
ZAC–4	FMNH 356606	H29	MXJ192	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
ZAC–5	FMNH 356607	H29	MXJ194	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
ZAC–6	FMNH 356608	H29	MXJ195	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
ZAC–7	FMNH 393835	H29	MXJ168	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
ZAC–8	FMNH 395772	H29	MXJ170	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
ZAC–9	FMNH 395773	H30	MXJ171	Mexico	Zacatecas	Valparaiso, 9 km N, 6 km W
Outgroup	MZFC	*Melanerpes pucherani*	CHIMA068	Mexico	Oaxaca	San Isidro La Gringa, a 1 km SE de San Francisco, La Paz
Outgroup	MZFC	*Melanerpes aurifrons*	CHIMA506	Mexico	Oaxaca	Chalchijapa, 2.3 km antes del pueblo en Galera
Outgroup	MZFC	*Melanerpes pygmaeus*	CONACYT 99-109	Mexico	Campeche	Tzotzil a 17 km W
Outgroup	MZFC	*Melanerpes pygmaeus*	CONACYT 99-160	Mexico	Campeche	Tachich a 7 km W
Outgroup	MZFC	*Melanerpes aurifrons*	CONACYT 99-036	Mexico	Campeche	Estación de Vida Silvestre Hampolol, 12 km N Campeche
Outgroup	MZFC	*Melanerpes aurifrons*	MEX095	Mexico	Veracruz	Sierra de Santa Martha, El Bastonal
Outgroup	MZFC	*Melanerpes uropygialis*	MEX185	Mexico	Sinaloa	Rancho Bequillos, Mocorito
Outgroup	MZFC	*Melanerpes lewis*	DHB2274	USA		
Outgroup	MZFC	*Sphyrapicus nuchalis*	QRO196	Mexico	Queretaro	Laguna de la Cruz
Outgroup	Genbank AY274057	*Coracias spatulatus*	CORSPA			
Outgroup	Genbank AF082060	*Coracias spatulatus*	CORSPA			

The Wilson Journal of Ornithology 120(3):494–498, 2008

DIET OF ACORN WOODPECKERS AT LA PRIMAVERA FOREST, JALISCO, MEXICO

VERONICA CAROLINA ROSAS-ESPINOZA,[1,2] ELISA MAYA-ELIZARRARAS,[1] OSCAR FRANCISCO REYNA BUSTOS,[1] AND FRANCISCO MARTIN HUERTA-MARTINEZ[1]

ABSTRACT.—We studied the diet of the Acorn Woodpeckers (*Melanerpes formicivorus*) at La Primavera Forest, Jalisco, Mexico. This resident species had a diverse diet throughout all seasons. The diet included acorns of *Quercus viminea*, *Q. castanea*, and *Q. laeta*, which were stored primarily in granaries in live trunks of pine (*Pinus* spp.) trees. They also consumed acorns of *Q. magnoliifolia* and *Q. resinosa* by piercing and eating just the central part of the seed. Acorn Woodpeckers did not use acorns from species of oak in the same proportion as available. They also fed seasonally on insects (Coleoptera and Lepidoptera) and tree sap. *Received 7 August 2006. Accepted 27 January 2008.*

Acorn Woodpeckers (*Melanerpes formicivorus*) have diversified diets and consume different food resources seasonally (MacRoberts 1970, Stacey 1981, Kattan 1988, Stanback 1989, Winkler et al. 1995). Acorns constitute a significant part of their diet (Koenig and Mumme 1987, Koenig et al. 1995, Koenig and Haydock 1999), and they feed extensively on mature and immature acorns before storage begins in fall (MacRoberts 1970). Acorns are stored in prepared holes (granaries) in the surfaces of oaks (*Quercus* spp.) and pines (*Pinus* spp.) for later use (Henshaw 1921, Ritter 1921, Skutch 1969, MacRoberts 1970). Large granaries are maintained by groups of woodpeckers that share in maintenance and consumption of stored acorns (Wong 1989). However, some populations store acorns in tree cracks and holes in trees while others do not store acorns (Skutch 1969, MacRoberts 1970, Stanback 1989, Arsenault 2004). Other reported foods are sap and insects in spring and summer and, occasionally, bird's eggs, epiphytes, lizards, and ants (MacRoberts 1970, Stacey and Jansma 1977, Koenig and Williams 1979, Stacey 1981, Kattan 1988, Ligon and Stacey 1989, Stanback 1989, Winkler et al. 1995, Koenig and Haydock 1999).

Acorn Woodpeckers occur from northwestern Oregon, south through California and Arizona, and throughout Mexico to northern Colombia (Benítez-Díaz 1993, Koenig et al. 1995, Winkler et al. 1995). The close association of these woodpeckers with oaks limits their geographic distribution (Koenig et al. 1995, Koenig and Haydock 1999). Acorn Woodpecker densities in the United States increase and population variability decreases with increasing abundance and diversity of oaks. This latter pattern has not been clearly found in the southwestern United States (Koenig and Haydock 1999). The objective of our study was to examine the diet of Acorn Woodpeckers in La Primavera Forest, Jalisco, Mexico.

METHODS

Study Area.—We studied Acorn Woodpeckers in La Primavera Forest in Jalisco State, west central Mexico (20° 32′ to 20° 44′ N, 103° 28′ to 103° 42′ W; 1,400 to 2,200 m above sea level). This forest comprises 30,500 ha and is largely (84%) dominated by oaks and pines (SEMARNAT 2000). The oak forest comprises an additional 7% of the area while the pine forest is dominated by *Pinus oocarpa*, which occupies 1% of the area. The remainder of the area is comprised of other lowland forests and riparian vegetation (SEMARNAT 2000). There are 11 species of oak (Table 1) (Reyna 2004) and five species of pine (*P. devoniana*, *P. douglasiana*, *P. lumholtzii*, *P. luzmariae*, *P. oocarpa*) at La Primavera Forest (SEMARNAT 2000). The distribution and abundance of oak and pine species in the oak-pine forest are not homogeneous (Olmo 2005). *Pinus oocarpa*, *Quercus magnoliifolia*,

[1] Centro Universitario de Ciencias Biologicas y Agropecuarias, Universidad de Guadalajara, km 15.5 carretera a Nogales, Zapopan, Jalisco 45110, Mexico.
[2] Corresponding author;
e-mail: Verorosas75@hotmail.com

TABLE 1. Characteristics of acorns at La Primavera Forest, Jalisco, Mexico (after Reyna 2004).

Species	Fruiting period	Acorn size (mm)	
		Width	Length
Quercus castanea	Aug–Oct	11–17	10–20
Q. coccolobifolia	Aug–Sep	5–8	8–10
Q. gentryi	Nov–Dec	1.5	15–20
Q. laeta	Sept–Feb	7–12	15–18
Q. magnoliifolia	Jul–Aug	10–25	20–30
Q. obtusata	Aug–Nov	10–20	10–20
Q. praineana	Jun–Sep	7–10	7–12
Q. resinosa	Jul–Nov	15–30	15–35
Q. rugosa	Oct–Feb	8–12	15–25
Q. subspathulata	Apr–May	8–10	22–24
Q. viminea	Jul–Oct	6–9	12–16

and *Q. resinosa* are abundant and have a homogeneous distribution in the entire forest, but other species of oaks are distributed altitudinally correlating with temperature and humidity. *Q. castanea* and *Q. laeta* are primarily distributed in the southwestern portion of the forest. The woodpecker community in the area is composed of seven species: *M. formicivorus* is the resident dominant species and there are five other resident woodpeckers (*Colaptes auratus*, *Melanerpes aurifrons*, *M. uropygialis*, *Picoides arizonae*, *P. scalaris*), and one migratory species (*Sphyrapicus varius*).

Data Collection.—We recorded field observations (32 hrs/month) of Acorn Woodpeckers in the oak-pine forest from June 2004 to July 2005. Woodpeckers were located by searches throughout suitable habitats and individuals were observed and followed. Frequently, we could simultaneously observe several individuals in the same area. We searched the oak-pine forest for granaries during December and January where the greatest woodpecker activity occurred. We recorded the species of tree, diameter at breast height (DBH), and counted the number of holes used for acorn storage at each granary. We removed acorns from the top, middle, and bottom of granaries for identification.

RESULTS

The diet of Acorn Woodpeckers in La Primavera Forest was diverse and varied seasonally. This woodpecker simultaneously used several food sources including insects, sap, and immature and mature acorns.

The main foraging activities of Acorn Woodpeckers during the rainy season (Jun–Aug) were 'hawking' beetles (Coleoptera) and butterflies (Lepidoptera) (38–40% of the total time) followed by feeding on sap (27–30%) and immature acorns (18–22%) (Fig. 1). Im-

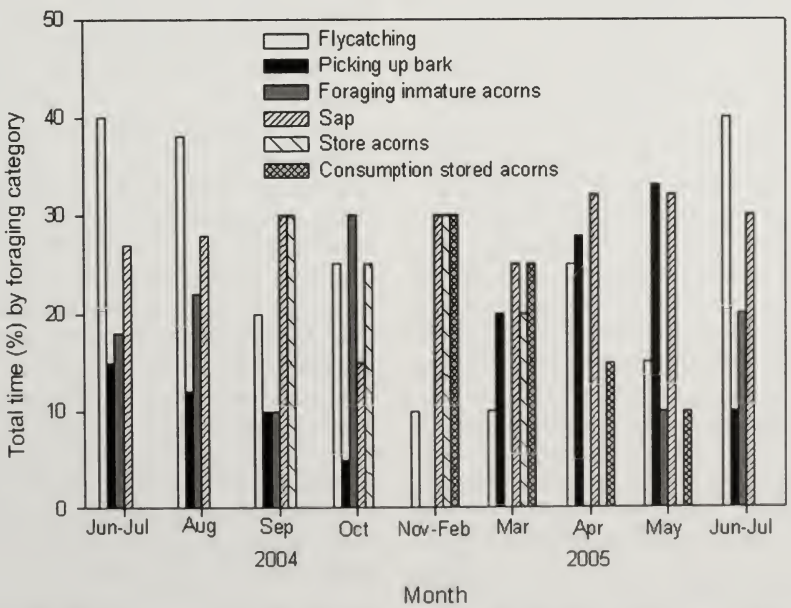


FIG. 1. Foraging time budgets for Acorn Woodpeckers at La Primavera Forest, Jalisco, Mexico, 2004–2005.

TABLE 2. Characteristics of granaries of Acorn Woodpeckers at La Primavera Forest, Jalisco, Mexico, 2004–2005. ($\bar{x}$ ± SD, n = 96).

Species used as granaries	Number of granaries	Tree condition (live/dead)	Average DBH (cm)	Acorn species stored
Pinus oocarpa	95	91/4	39.23 ± 13.25	*Quercus viminea* *Q. castanea* *Q. laeta*
Quercus castanea	1	1/0	32	*Q. castanea* *Q. laeta*

mature acorns of *Q. magnoliifolia* and *Q. resinosa* were consumed most frequently but their consumption diminished after start of the rainy season. Acorns of these oaks are large (Table 1), and woodpeckers pierced and ate the central part of the seed. We did not find acorns of these species in granaries. We also observed individual Acorn Woodpeckers foraging on immature acorns and, possibly, obtaining insects and grit on the ground.

Acorn Woodpeckers stored acorns from late August to early March and of primarily three species: *Q. viminea*, *Q. castanea*, and *Q. laeta* which are characterized by acorns of small size (Table 1). *Quercus gentryi* also had a small acorn but was not found in granaries, probably because of its lower density in the forest and low availability of acorns. Acorn Woodpeckers increased their consumption of stored acorns from November to February, which continued into April (Fig. 1). Woodpeckers consumed butterflies (Lepidoptera) (captured by hawking) and beetle (Coleoptera) larvae (from the bark of trunks of *P. oocarpa*) (20–33% of total time), fed on sap (25–32%), and consumed stored acorns (10–25%) during the hot dry season (Mar to May) (Fig. 1).

We found nests of Acorn Woodpeckers with young before fledging from mid June to late July at La Primavera Forest. We observed medium size groups (6–8 individuals) and one group of 10 individuals after early July. These groups regularly contained three or four young. We observed several smaller groups (2–3 individuals) in the area from late February to early March. These medium size groups maintained granaries, mainly in live trunks of pine trees (Table 2). Granaries in the southwestern portion (oak-pine forest) of the forest were filled with acorns of *Q. castanea* and *Q. laeta* (n = 32) while granaries in the remainder of the forest were filled with acorns of *Q. viminea* (n = 64). Granaries with acorns of *Q. castanea* and *Q. laeta* had a small number of holes, and acorns of *Q. viminea* were stored more often in tree cracks than in granaries. The average (± SD) number of holes per granary was 1,267.11 ± 1,427 with 853.71 ± 1,068.81 containing acorns (n = 96).

DISCUSSION

Acorn Woodpeckers in La Primavera Forest had a diverse diet similar to those reported for Acorn Woodpeckers in North (MacRoberts 1970, Stacey 1981) and Central America (Kattan 1988). Unlike what has been reported in Colombia (Kattan 1988), we did not observe Acorn Woodpeckers consuming fruits other than acorns, or feeding on flower nectar. These results suggest that Acorn Woodpecker diets were greatly affected by the abundant sources of acorns. Seasonal availability and use of resources by Acorn Woodpeckers decreases from temperate to tropical regions. Sap is greatly consumed in spring, insects in summer, and acorns during fall and winter in North America (MacRoberts 1970). Acorn Woodpeckers in La Primavera Forest simultaneously use several food sources seasonally while in Central America, the diet is more diverse because more food sources are available (Kattan 1988).

The number of oaks (5 species) used by Acorn Woodpeckers in La Primavera Forest is larger than reported in North and South America (MacRoberts 1970, Stacey and Jansma 1977, Stacey 1981, Kattan 1988, Stanback 1989, Koenig and Benedict 2002, Arsenault 2004). Our results revealed that immature and mature acorns are an important component of the diet of this woodpecker. This may allow

the Acorn Woodpecker to be resident in La Primavera Forest as a large number of oak species increases the probability of finding sufficient food resources, even if a crop failure occurs in a particular species of oak (Bock and Bock 1974, Koenig and Haydock 1999). There is decreasing use of acorns in the diet (Kattan 1988, Wong 1989) of Acorn Woodpeckers from North to South America, because this food item may be replaced by other available resources including fleshy fruit, nectar, and flower catkins as in Colombia (Kattan 1988). This may be related to the decreasing number of filled holes in granaries from North to South America. Trees contain thousands of holes in temperate zones (MacRoberts 1970), but this number decreases in tropical areas such as La Primavera Forest ($\bar{x}$ = 1,267 holes) to 16 to 20 in Belize (Stacey 1981) with no storage of acorns in the Colombian Andes (Kattan 1988). The long period during which acorns are available for harvesting in La Primavera Forest suggests that importance and necessity of acorn storage is decreased compared to more temperate areas. Piercing and eating of the central part of large acorns without storage has also been reported by Stanback (1989) in Costa Rica with *Q. costaricensis*. This increases the foraging flexibility of Acorn Woodpeckers (Stanback 1989).

MacRoberts and MacRoberts (1976) and Stacey and Bock (1978) suggested that group size of Acorn Woodpeckers is large in areas with high numbers of species of oaks. However, we observed medium size groups of Acorn Woodpeckers in La Primavera Forest. We expected groups at least of medium size given the importance of acorns in their diet, and given that group size is related to maintenance of granaries (MacRoberts and MacRoberts 1976, Stacey 1979).

Acorn Woodpeckers at La Primavera Forest used live pines (*P. oocarpa*) for granaries, mainly in the surfaces of trunks or in pre-existing tree cracks. This may be the result of the availability of live pines and their life expectancy compared with snags. Use of pine trees as granaries has also been reported in Durango, Mexico where granaries were constructed in *P. engelmannii* with a similar DBH (37.4 ± 10.6 cm) (Koenig and Williams 1979) as in our study area.

Koenig and Benedict (2002) reported the three species of oaks present at the Hastings Reservation in central coastal California had differential use as granaries. In contrast, not all oaks (11 total species) were used as granaries in La Primavera Forest. Acorn Woodpeckers appear to differentially and selectively use five oak species. This could be a consequence of tree density, acorn production by species, size and nutrient quality, and content of secondary metabolites in acorns (Koenig and Benedict 2002).

ACKNOWLEDGMENTS

We thank Manuel Anguiano-Santana, Luz María Hinojosa-Medina, and Aleyda Barraza for field assistance, and the Executive Committee of La Primavera Forest for assistance with logistics. We thank Cecilia Neri-Luna for improving the manuscript.

LITERATURE CITED

Arsenault, D. P. 2004. Differentiating nest-sites of primary and secondary cavity-nesting birds in New Mexico. Journal of Field Ornithology 75: 257–265.

Benitez-Diaz, H. 1993. Geographic variation in coloration and morphology of the Acorn Woodpecker. Condor 95:63–71.

Bock, C. E. and J. H. Bock. 1974. Geographical ecology of the Acorn Woodpecker: abundance vs. diversity of resources. American Naturalist 108: 694–698.

Henshaw, H. W. 1921. The storage of acorns by the California Woodpecker. Condor 23:109–118.

Kattan, G. 1988. Food habits and social organization of Acorn Woodpeckers in Colombia. Condor 90: 100–106.

Koenig, W. D. and L. S. Benedict. 2002. Size, insect parasitism, and energetic value of acorns stored by Acorn Woodpeckers. Condor 104:539–547.

Koenig, W. D. and J. Haydock. 1999. Oak, acorns, and the geographical ecology of Acorn Woodpeckers. Journal of Biogeography 26:159–165.

Koenig, W. D. and R. L. Mumme. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton University Press, Princeton, New Jersey, USA.

Koenig, W. D. and P. L. Williams. 1979. Notes of the status of the Acorn Woodpeckers in central Mexico. Condor 81:317–318.

Koenig, W. D., P. B. Stacey, M. T. Stanback, and R. L. Mumme. 1995. Acorn Woodpecker (*Melanerpes formicivorus*). The birds of North America. Number 194.

Ligon, J. D. and P. B. Stacey. 1989. On the significance of helping behavior in birds. Auk 106:700–705.

MacRoberts, M. H. 1970. Notes on the food habits and food defense of the Acorn Woodpecker. Condor 72:196–204.

MacRoberts, M. H. and B. R. MacRoberts. 1976. Social organization and behavior of the Acorn Woodpecker in central coastal California. Ornithological Monographs 21:1–115.

Olmo, G. B. 2005. Criterios e indicadores para la restauración del área de protección de flora y fauna La Primavera, Jalisco, México. Thesis. Universidad de Guadalajara, México.

Reyna, B. O. F. 2004. Arboles y arbustos del bosque La Primavera, guia ilustrada. Universidad de Guadalajara, CONABIO, Mexico.

Ritter, W. E. 1921. Acorn-storing by the California Woodpecker. Condor 23:3–14.

SEMARNAT (Secretaria de Medio Ambiente y Recursos Naturales). 2000. Programa de manejo area de protección de flora y fauna La Primavera. Subdireccion. General de Conservacion y Manejo de Areas Naturales Protegidas. CONANP, D. F., Mexico.

Skutch, A. 1969. Life-histories of Central American birds. III. Pacific Coast Avifauna 35.

Stacey, P. B. 1979. Habitat saturation and communal breeding in the Acorn Woodpecker. Animal Behavior 27:1153–1166.

Stacey, P. B. 1981. Foraging behavior of the Acorn Woodpecker in Belize, Central America. Condor 83:336–339.

Stacey, P. B. and C. E. Bock. 1978. Social plasticity in the Acorn Woodpecker. Science 202:1298–1300.

Stacey, P. B. and R. Jansma. 1977. Storage of piñon nuts by the Acorn Woodpecker in New Mexico. Wilson Bulletin 89:150–151.

Stanback, M. T. 1989. Observations on food habits and social organization of Acorn Woodpeckers in Costa Rica. Condor 91:1005–1007.

Winkler, H., D. A. Christie, and D. Nurney. 1995. Woodpeckers, an identification guide to the woodpeckers of the world. Houghton Mifflin Company, Boston, Massachusetts and New York, USA.

Wong, M. 1989. The implications of germinating acorns in the granaries of Acorn Woodpeckers in Panama. Condor 91:724–726.

The Wilson Journal of Ornithology 120(3):499–504, 2008

SEASONAL VARIATION IN ACOUSTIC SIGNALS OF PILEATED WOODPECKERS

SARAH B. TREMAIN,[1,2] KYLE A. SWISTON,[1] AND DANIEL J. MENNILL[1]

ABSTRACT.—We used remote recorders to document temporal variation in acoustic signals of a population of Pileated Woodpeckers (*Dryocopus pileatus*) along the Choctawhatchee River in the Florida Panhandle, sampling seven different locations for 24 hrs once a week between mid January and mid April 2006. We found significant seasonal variation in the drumming behavior and vocal behavior of Pileated Woodpeckers. Drumming behavior peaked in mid March, just prior to onset of breeding activities. The three primary long-distance Pileated Woodpecker vocalizations, the *cackle* call, the *wuk* series call, and the *wok* call had similar patterns of seasonal variation. All four acoustic signals declined to low levels by early April when birds were nesting. The seasonal pattern of variation for all four Pileated Woodpecker acoustic signals had a similar pattern to that observed for song in many temperate passerines, and support the hypothesis that woodpecker calls and drumming displays are the functional counterparts to passerine song. *Received 17 September 2007. Accepted 27 January 2008.*

The long-range acoustic signals of many territorial birds function in both territory defense and mate attraction (Catchpole and Slater 1995). Comparatively little research has been conducted on acoustic communication in woodpeckers (Piciformes) (Stark et al. 1998). The functions of the majority of acoustic signals used by woodpeckers are not fully understood, and seasonal patterns of variation in their acoustic behavior have yet to be investigated. A clear understanding of seasonal variation in woodpecker acoustic signals may increase our understanding of the function of their calling and drumming behavior.

Woodpecker vocalizations remain virtually unstudied, although woodpecker mechanical sounds have received modest attention (Stark et al. 1998). All woodpeckers produce nonvocal acoustic signals referred to as "drumming" and these far-carrying sounds are thought to function in long distance communication (Dodenhoff et al. 2001). A woodpecker drum consists of a repetitive series of strikes by the bird's bill against an external substrate, and is distinguished as not being associated with foraging or cavity excavation (Bent 1939, Pynnönen 1939, Short 1974). Woodpecker drumming is postulated to be the evolutionary counterpart to song (Pynnönen 1939, Lawrence 1967), replacing the complex vocalizations used by passerines for long-distance communication (Dodenhoff et al. 2001). Several hypotheses for the function of drumming have been proposed; the best supported include territory announcement and maintenance, mate attraction, pair bond maintenance, and individual localization (Short 1982, Wilkins and Ritchison 1999).

Pileated Woodpeckers (*Dryocopus pileatus*) are sexually dimorphic, monogamous, nonmigratory woodpeckers that inhabit deciduous and coniferous forests from southern Canada through the western, midwest, and eastern United States (Bent 1939, Bull and Jackson 1995). The ecology of Pileated Woodpeckers has been studied in greater detail than many other woodpecker species, perhaps owing to their majestic appearance, large size, and wide distribution. The basic characteristics of Pileated Woodpecker drums have been described (Bull and Jackson 1995, Stark et al. 1998), although a detailed study of variation in drumming behavior over time has not been previously conducted. Additionally, there are discrepancies regarding vocalizations, especially concerning terminology and function (Humphrey 1946, Kilham 1959).

We recorded the acoustic signals of a population of Pileated Woodpeckers along the Choctawhatchee River in the Florida panhandle over a 4-month period. Our objective was to examine seasonal patterns in the acoustic behavior of this species to better understand the possible functions of both vocal and nonvocal acoustic communication in woodpeckers. We predicted that acoustic signals of Pileated Woodpeckers would show a peak in activity at the start of the breeding season, sim-

[1] Department of Biological Sciences, University of Windsor, Windsor, ON N9B 3P4, Canada.

[2] Corresponding author; e-mail: tremai5@uwindsor.ca

ilar to the documented pattern of seasonal variation in singing behavior of many songbirds (e.g., Catchpole 1973, Amrhein et al. 2004).

METHODS

Field Techniques.—We studied Pileated Woodpeckers in a plot of mature bottomland forest along the Choctawhatchee River in the Florida Panhandle (30° 3′ N, 85° 5′ W), during a bioacoustic search for Ivory-billed Woodpeckers (*Campephilus principalis*) (Hill et al. 2006). We placed seven automated "listening stations" throughout our study site in January 2006. Each listening station consisted of a Sennheiser ME-62 omni-directional microphone and K6 power module connected to a Marantz PMD-670 solid-state digital recorder powered by a sealed lead-acid battery. The microphones were shielded in protective rain guards made from polyvinyl chloride (PVC) tubing and were attached to the top of a 3-m wooden stake via a 30-cm shelf bracket. Wooden stakes were attached to small trees in an effort to capture sound from all directions and minimize any sound shadow resulting from the tree trunk. All visible materials were camouflaged with spray paint to minimize the influence of their presence on the behavior of resident birds. Each of the seven listening stations recorded 24-hr MP3 files at 44.1 kHz, 16 bit, 160 kbps onto Hitachi 3GB microdrive cards. Memory cards and batteries were changed daily by quietly paddling or hiking to the site. Full details of the recording apparatus and sampling regime are given in Hill et al. (2006).

We selected recordings from 14 dates between 20 January and 20 April 2006 (specific recording dates: 20, 27 Jan; 3, 10, 16, 22, 28 Feb; 7, 14, 22, 28 Mar; and 5, 14, 20 Apr). We used recordings from seven distinct areas on each of the 14 dates which yielded 98 24-hr recordings. The recordings analyzed were selected from days with no precipitation and little to no wind to ensure consistency in recording conditions. Files were scanned using Syrinx-PC sound analysis software (John Burt, Seattle, WA, USA) and acoustic signals of interest were annotated using Syrinx-PC's time and frequency cursors.

The seven recording units were separated by a distance of 766.4 ± 83.2 m ($\bar{x}$ ± SE) between the seven microphones. The territory size of Pileated Woodpeckers has not been carefully described, but reported breeding densities in bottomland forests of the southern United States are one pair/14–43 ha (Tanner 1942, Dennis 1951, Carter 1967). Consequently, we assume that each one of the seven recording units was recording different individuals.

We collected direct observations of birds on the Choctawhatchee River to assess the timing of Pileated Woodpecker breeding behavior. A team of field technicians searching for Ivory-billed Woodpeckers from January to May 2006 and 2007 documented any Pileated Woodpecker breeding behavior observed. We also referred to published records of the timing of Pileated Woodpecker breeding. We collected average daily temperature data throughout the recording period from www.accuweather.com.

Definition of Drums and Vocalizations.—The Pileated Woodpecker drum pattern is a tattoo of 11–30 beats lasting ~3 sec and trailing off in amplitude towards the end (Kilham 1959; Fig. 1A). Birds also produce a quieter "drum-tapping" which is a slow, close-range communication that can be heard during times of feeding, courtship, and upon agreement regarding the location of a nest hole (Kilham 1959). Many other woodpecker species present at our study site engaged in similar forms of drum-tapping, and we omitted drum-tapping given the difficultly in accurately distinguishing between Pileated Woodpecker and heterospecific tapping without visual identification.

Pileated Woodpecker vocalizations have been described by several authors, notably Kilham (1959) and Short (1982), although terminology is inconsistent across authors. Kilham (1959) described five basic calls while Short described three. However, across all descriptions, Pileated Woodpecker vocalizations are simple acoustic signals, consisting of 1–2 syllables given individually or in series (Bull and Jackson 1995). We examined temporal patterns in the three most common long-distance Pileated Woodpecker vocalizations: (1) the *cackle* (also referred to as a fast *wuk* series call), (2) the *wuk* series call, and (3) the *wok* call (also referred to as the *waa* call). The *cackle* call (Fig. 1B) consists of rapid series

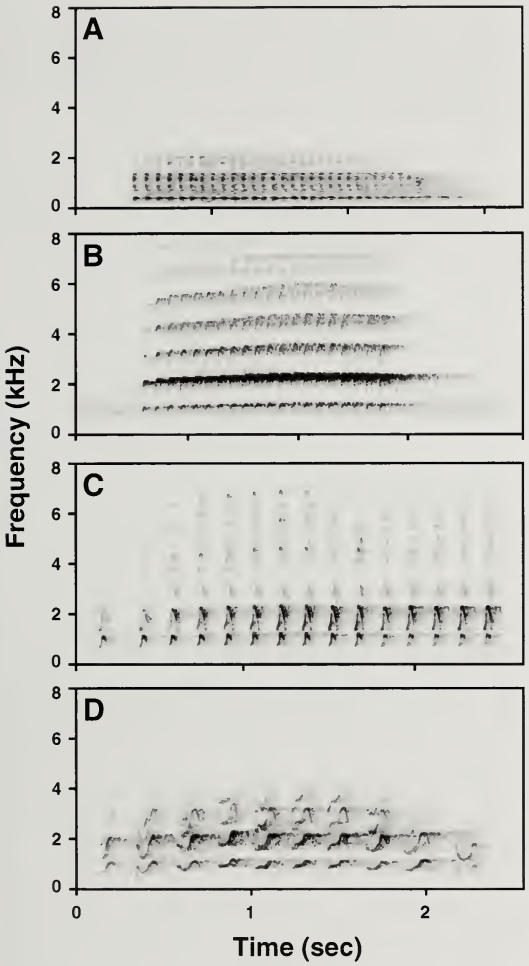


FIG. 1. Sound spectrograms of four primary long-distance acoustic signals of Pileated Woodpeckers sampled with automated recorders in the Choctawhatchee River bottomland forests in Florida: (A) drumming, (B) the *cackle* call, (C) the *wuk* series call, and (D) the *wok* call.

of notes that rise and then fall in pitch. Capable of transmitting over long distances, it is thought to be used in territorial assertion, distant interactions, and as a copulation readiness signal (Short 1982). The *wuk* series call (Fig. 1C) described by Short (1982), is a much longer series of spaced-out notes. Some authors categorize the *cackle* call as a fast version of the *wuk* series call, but we distinguish the *wuk* as the substantially slower, drawn-out calls. The *wuk* series is used in situations of agitation or alarm (Bull and Jackson 1995). The *wok* call (Fig. 1D) described by Short (1982), is a lower amplitude vocalization generally given in a series of eight notes, at a rate of ~3 notes/sec. It is used during interactions between birds and appears to be synonymous with Kilham's (1959) "high call".

Statistical Analysis.—We applied repeated measures ANOVA using SPSS 14 to analyze temporal patterns in each of the four Pileated Woodpecker acoustic signals (SPSS Inc., Chicago, IL, USA). The within-subjects factor for each acoustic signal was the week number (14 levels), and the between-subjects factor was the recording location (7 levels). Values for each acoustic signal were calculated as the mean frequency of occurrence per hour across all daylight hours. Results are given as means ± SE and all tests are two-tailed.

RESULTS

Pileated Woodpeckers in the Choctawhatchee River bottomlands demonstrated significant seasonal variation in all four of this species' long-range acoustic signals. Drum production remained low throughout January and February, increased in early March, peaked in late March, and decreased to the January and February level by the beginning of April (ANOVA: $F = 2.49$, $P = 0.007$; Fig. 2A). The frequency of occurrence of the *cackle* call increased from the end of January to a peak in mid March, followed by a decrease which continued into mid April (ANOVA: $F = 4.50$, $P < 0.001$; Fig. 2B). The *wuk* series call exhibited substantial variation from week to week, but it followed an oscillating pattern which peaked in late March, before decreasing substantially in April (ANOVA: $F = 2.58$, $P = 0.005$; Fig. 2C). The *wok* call at all times of year was less frequent than all other call types (Fig. 2). There was an increase in the frequency of occurrence for the *wok* call from January to mid March; after this date the *wok* call was not detected again until early April when levels increased once again, albeit at a low level (ANOVA: $F = 2.70$, $P = 0.003$; Fig. 2D).

Pileated Woodpeckers were abundant at the study site and were encountered daily throughout the period from January to April. Pileated Woodpecker breeding activities were observed on four occasions; (1) one pair of birds excavated a cavity between 20 and 23 March (cavity excavation is believed to last

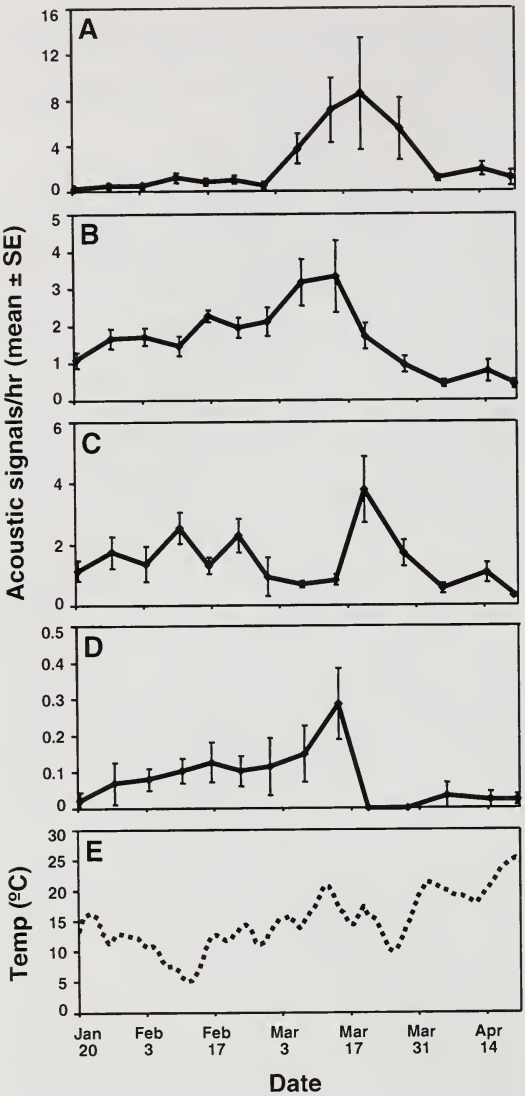


FIG. 2. Seasonal variation in frequency of recording the four primary long-distance acoustic signals of Pileated Woodpeckers in the Choctawhatchee River bottomland forests in Florida: (A) drumming, (B) the *cackle* call, (C) the *wuk* series call, and (D) the *wok* call. Seasonal variation in temperature (E) shows a gradually increasing mean temperature across the recording period.

~3–6 weeks); (2 and 3) two different nests were found, both with incubating parents, on 3 and 5 May (incubation is believed to last 18 days, suggesting eggs in these nests were laid in Apr); and (4) for a fourth pair fledglings were observed in early May (suggesting eggs were laid in late Mar or early Apr). This period of nesting and egg laying activity in late March and April corresponds to a period when the temperature on the Choctawhatchee River was beginning to increase (Fig. 2E).

DISCUSSION

Our recordings from the bottomland forests along the Choctawhatchee River in the Florida Panhandle revealed significant seasonal variation in the acoustic behavior of Pileated Woodpeckers. All four of the Pileated Woodpecker's long-distance acoustic signals reached a peak in mid March. Pileated Woodpeckers in Florida commenced breeding in mid March; other studies have found that egg laying occurs between 17 March and 25 May in Florida (Bent 1939, Stevenson and Anderson 1994). Our observations confirmed that mid March and early April mark the beginning of the breeding period for the Choctawhatchee Pileated Woodpecker population. Our results support the prediction that acoustic signals peak in activity at the start of the breeding season. The pattern we observed for all four Pileated Woodpecker acoustic signals corresponds to the pattern of seasonal variation documented for the singing behavior of many songbirds (e.g., Catchpole 1973, Amrhein et al. 2004).

All four of the long-range signals of Pileated Woodpeckers that we studied were given at low levels throughout late January and February. Pileated Woodpecker pairs are territorial at all times of the year (Hoyt 1957, Bull and Jackson 1995) and this early winter period corresponds with pre-breeding activities when males and females have not yet started excavating nest cavities. The *wuk* series call followed a non-linear pattern during this period of low vocal activity, which may be related to the proposed function of this call. This acoustic signal is thought to be given as an alarm call or when a bird is agitated (Bull and Jackson 1995). The stochastic pattern of variation we observed for the *wuk* series call likely relates to the stochastic nature of threats that may have elicited alarm. Both the *cackle* call and *wok* call increased in frequency in early March, reaching their peak in mid March. Both the drum and the *wuk* series call reached their maximum the following week. Drumming is believed to function in territorial announcement (Lawrence 1967); this maximum

presumably occurred because adults were actively defending their territory and nest site at the time of intensified courtship and egg laying. A decrease occurred in the production of all four acoustic signals in late March. Egg-laying has been documented to occur in Florida between 17 March and 25 May (Bent 1939), and this minimum in acoustic signal production may have occurred because females were incubating their clutches; high levels of calling may increase birds' conspicuousness and reveal the location of their nest hole to predators.

The drum display, *cackle* call, and the *wok* call had a similar pattern of seasonal variation, suggesting that all three signals have roles of increased importance during the breeding season. The drum and *cackle* call of the Pileated Woodpecker have both been proposed to function in territorial advertisement; both males and females have been observed to respond to territorial intrusion by drumming and calling (Mellen et al. 1992). Pileated Woodpecker pairs defend territories all year, but do not defend their territories as vigorously during the non-breeding season in the fall and winter; during this time territorial intrusion by floaters is generally tolerated (Bull and Jackson 1995). The seasonal patterns we observed in both the drum and *cackle* calls of Pileated Woodpeckers in northern Florida reflect this increase in territorial aggression with hourly rates starting low during the pre-breeding season in January and mid February before peaking during the onset of breeding in mid March. The *wok* call is usually given in interactions between individuals, which should similarly reach a maximum during the period of affiliation associated with the start of the breeding season. Understanding how these vocalizations vary across the breeding season has important implications for survey techniques (Selmi and Boulinier 2003); our data show that Pileated Woodpeckers should be most readily detectable early in the breeding season.

Woodpecker drumming has long been postulated to be the functional counterpart to passerine song (Pynnönen 1939, Lawrence 1967). Our analyses reveal a pattern of seasonal variation in drumming behavior, as well as calling behavior, that supports this hypothesis. Drumming has received modest attention in the literature (Stark et al. 1998, Dodenhoff et al. 2001), but more quantitative work is needed to clarify possible functions.

ACKNOWLEDGMENTS

We thank G. E. Hill, B. W. Rolek, and the many members of the Ivory-billed Woodpecker search team for assistance in the field. We thank R. D. Stark and an anonymous reviewer for comments on the manuscript. We thank the Natural Sciences and Engineering Research Council of Canada (NSERC), Canada Foundation for Innovation, Ontario government, and the University of Windsor for supporting DJM's research program. We also thank NSERC, Pelee Island Winery, Nokuse Plantation Inc. and M. C. Davis, Northwest Florida Water Management District, Florida Fish and Wildlife Conservation Commission, U.S. Fish and Wildlife Service, and Marantz Canada for supporting the Florida search for Ivory-billed Woodpeckers, which gave rise to the data in this study.

LITERATURE CITED

Amrhein, V., H. P. Kunc, and M. Naguib. 2004. Seasonal patterns of singing activity vary with time of day in the Nightingale (*Luscinia megarhynchos*). Auk 121:110–117.

Bent, A. C. 1939. Life histories of North American woodpeckers. U.S. National Museum Bulletin Number 174.

Bull, E. L. and J. A. Jackson. 1995. Pileated Woodpecker (*Dryocopus pileatus*). The birds of North America. Number 148.

Carter, W. A. 1967. Ecology of the nesting birds of the McCurtain Game Preserve, Oklahoma. Wilson Bulletin 79:259–272.

Catchpole, C. K. 1973. The functions of advertising song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and Reed Warbler (*Acrocephalus scirpaceus*). Behaviour 46:300–320.

Catchpole, C. K. and P. J. B. Slater. 1995. Bird song: biological themes and variations. Cambridge University Press, New York, USA.

Dennis, J. V. 1951. A comparative study of Florida woodpeckers in the nonbreeding season. Thesis. University of Florida, Gainesville, USA.

Dodenhoff, D. J., R. D. Stark, and E. V. Johnson. 2001. Do woodpecker drums encode information for species recognition? Condor 103:143–150.

Hill, G. E., D. J. Mennill, B. W. Rolek, T. J. Hicks, and K. A. Swiston. 2006. Evidence suggesting that Ivory-billed Woodpeckers (*Campephilus principalis*) exist in Florida. Avian Conservation and Ecology 1(3):2.

Hoyt, S. F. 1957. The ecology of the Pileated Woodpecker. Ecology 39:246–256.

Humphrey, P. S. 1946. Observations at the nest of a Pileated Woodpecker. Migrant 17:43–46.

Kilham, L. 1959. Behavior and methods of communication of Pileated Woodpeckers. Condor 61: 377–387.

Lawrence, L. de K. 1967. A comparative life-history

study of four species of woodpeckers. Ornithological Monographs Number 5.

Mellen, T. K., E. C. Meslow, and R. W. Mannan. 1992. Summertime home range and habitat use of Pileated Woodpeckers in western Oregon. Journal of Wildlife Management 56:96–103.

Pynnönen, A. 1939. Beiträge zur Kenntnis der Biologiefinnisher Spechte. Annales Botanici Societatis Zoologicae Botanicae Fennicae Vanamo 7:1–166.

Selmi, S. and T. Boulinier. 2003. Does time of season influence bird species number determined from point-count data? A capture-recapture approach. Journal of Field Ornithology 74:349–356.

Short, L. L. 1974. Habits and interactions of North American three-toed woodpeckers (*Picoides arcticus* and *Picoides tridactylus*). American Museum Novitates 547(2):1–42.

Short, L. L. 1982. Woodpeckers of the world. Delaware Museum of Natural History Monographs, Series Number 4.

Stark, R. D., D. J. Dodenhoff, and E. V. Johnson. 1998. A quantitative analysis of woodpecker drumming. Condor 100:350–356.

Stevenson, H. M. and B. H. Anderson. 1994. The birdlife of Florida. University of Florida Press, Gainesville, USA.

Tanner, J. T. 1942. The Ivory-billed Woodpecker. Research Report Number 1. National Audubon Society, New York, USA.

Wilkins, H. D. and G. Ritchison. 1999. Drumming and tapping by Red-bellied Woodpeckers: description and possible causation. Journal of Field Ornithology 70:578–586.

The Wilson Journal of Ornithology 120(3):505–512, 2008

COMMON POORWILL ACTIVITY AND CALLING BEHAVIOR IN RELATION TO MOONLIGHT AND PREDATION

CHRISTOPHER P. WOODS[1,2] AND R. MARK BRIGHAM[1,3]

ABSTRACT.—We investigated the influence of lunar and environmental factors on behavior of Common Poorwills (*Phalaenoptilus nuttallii*) in southern Arizona under a diverse set of natural and artificial conditions. Radio-marked poorwills were most active shortly after sunset during the new moon. Movements declined as evening progressed. Activity remained high for several hours after sunset when the moon was full. Poorwills were heard calling from March through October, but most calling occurred between early May and September. Only ambient light was correlated with number of poorwills heard calling. More poorwills responded to playbacks of conspecifics when the moon was full than when it was new. Poorwills did not change their response to conspecifics during full moon when playback of poorwill calls followed playback of Great Horned Owl (*Bubo virginianus*) calls but, during the new moon, fewer birds responded following the owl call. Poorwill behavior is strongly influenced by lunar conditions; their ability to detect and evade predators is important when calling advertises their location. *Received 22 May 2006. Accepted 1 September 2006.*

The behavioral influence of sunlight on birds is evident, but the influence of moonlight on diurnal and nocturnal birds is less apparent. For example, many nocturnal birds call most actively at dusk in contrast to the well known singing or calling at dawn by diurnal birds (Brauner 1952, Cooper 1981, Ganey 1990). Frequencies of calling, as well as overall activity patterns, are less well known during true night, when moonlight is the primary source of illumination. Some animals that are eaten by owls limit activity during periods when the moon is full (Price et al. 1984, Brown et al. 1988, Kotler et al. 1994, Brigham et al. 1999, Beier 2005, Lang et al. 2006). Bright moonlight coincides with the highest rates of nocturnal predation on Black-vented Shearwaters (*Puffinus opisthomelas*) and Cassin's Auklets (*Ptychoramphus aleuticus*) by Western Gulls (*Larus occidentalis*) (Nelson 1989, Keitt et al. 2004). Predation by Great Black-backed Gulls (*Larus marinus*) on Manx Shearwaters (*Puffinus puffinus*) is also strongly influenced by lunar condition (Brooke 1990). The behavioral effects of different lunar conditions are not universal, however, and other nocturnal animals increase activity when the moon is full and the sky is relatively bright, presumably because visual constraints are reduced during those periods (Cooper 1981, Mills 1986, Brigham and Barclay 1992, Jetz et al. 2003).

The Caprimulgidae is a circumglobal family of visually acute, crepuscular or nocturnal insectivores for which some aspects of lunar influence have been evaluated. The most commonly studied aspect of caprimulgid biology in the context of lunar illumination is the possible synchrony of breeding with lunar cycle (Jackson 1985, Mills 1986, Brigham and Barclay 1992, Perrins and Crick 1996). The hypothesis that light levels constrain foraging activity has also been proposed (Csada et al. 1992, Bayne and Brigham 1995, Jetz et al. 2003). Common Poorwills (*Phalaenoptilus nuttallii*; hereafter poorwill) are the smallest North American caprimulgid (45–50 g), and are one of the least understood of all North American birds, principally because of their cryptic coloration and nocturnal habits (Csada and Brigham 1992). We studied Common Poorwills under a diverse set of natural and artificial conditions to assess the influence of environmental and lunar factors on their behavior. Specifically, we compared the likelihood of movement by radio-marked birds between the full and new moons, and measured the rate of vocalization under a range of environmental, lunar, and seasonal situations. We also used playbacks of poorwill and Great Horned Owl (*Bubo virginianus*) vocalizations to examine whether the proximity to a potential predator influences calling responses by poorwills.

[1] Department of Biology, University of Regina, Regina, SK S4S 0A2, Canada.

[2] Current address: 11181 West Seneca Drive, Boise, ID 83709, USA.

[3] Corresponding author; e-mail: mark.brigham@uregina.ca

METHODS

We collected data during 1996–1999 at three sites within 100 km of Tucson, Arizona, USA: the National Audubon Society's Appleton-Whittell Research Ranch (31° 36′ N, 110° 30′ W), central portions of the Buenos Aires National Wildlife Refuge (31° 41′ N, 111° 26′ W), and the east side of the Tortolita Mountains (32° 32′ N, 111° 00′ W). All three sites are within the Sonoran desert ecosystem and share environmental and ecological attributes, including an elevation range of 1,000 to 1,550 m, hot days and cool nights, limited rainfall that typically occurs during the summer monsoon, and an abundance of cacti. Poorwills occurred year-round at the Tortolita and Buenos Aires sites; some over-wintered at the Research Ranch site, although most were absent during the coldest months.

Poorwills were captured at night either using mist nets in conjunction with playbacks of territorial calls or with a spotlight and long-handled net (Swenson and Swenson 1977, Jackson 1984, Brigham 1992). A few birds were captured or recaptured during daylight by flushing them into mist nets placed near roosts. Captured birds were banded with a USGS metal band and fitted with a temperature-sensitive radio transmitter (2 models that differed in mass and range were used: Model PD-2T, 2.8 g and 1–4 km range, and Model BD-2GT, 1.7 g and 0.5–2 km range; Holohil Systems Inc., Carp, ON, Canada). Transmitters were affixed using an elastic harness slipped over the wings (Brigham 1992, Hill et al. 1999).

Likelihood of Activity.—Radio-marked poorwills were monitored remotely using a Lotek SRX 400 Telemetry Receiver (Lotek Engineering Inc., Newmarket, ON, Canada) to assess activity patterns by quantifying variation in signal strength. Activity can be inferred because signal strength of successive radio pulses varies widely when radio-marked animals are active due to rapid changes in orientation of the transmitting antenna (Sutter et al. 1996, Brigham et al. 1999).

We evaluated the relationship between time of night, lunar illumination, and movement by poorwills using telemetry data from 5-min periods exactly 1, 3, and 5 hrs past sunset on nights for which there was either a full moon (>95% of the moon's face illuminated; 82 bird-nights from 6 males, 5 females, and 2 unknown gender juveniles) or no moon (<5% of the moon's face illuminated; 92 bird-nights from 9 males, 4 females, and 2 unknown gender juveniles). We only used data from birds that were euthermic (i.e., not torpid based on body temperature above 30° C) and for which there was either movement or inactivity in at least one of the 5-min periods. We inferred that movement had occurred when the standard deviation of the intensity of three signals recorded by the Lotek receiver was >10. This value was derived from comparisons of variation in signal strength when movement or inactivity by birds could be observed directly (cf. Sutter et al. 1996, Brigham et al. 1999). We used Chi-square tests to evaluate whether there were differences in the number of times that movement occurred during each 5-min period, for the two different lunar conditions.

Environmental Influences on Vocalization.—We examined the influence of climatic, lunar, and seasonal variables on poorwill vocalization by conducting night-time counts of calling poorwills at established points in the three study sites. Counts were made on 89 survey nights between June 1996 and January 1999, although effort varied seasonally and between sites. Most surveys, especially during spring and summer, were at 7 to 10 day intervals, but logistics meant that five were separated from a prior survey by only 2 to 4 days and 10 were separated by 2 weeks to 10 months. Two counts were done on 55 of 89 survey nights with 1–3 hrs separating each count making for 144 total counts. Poorwills were counted at the Research Ranch and Buenos Aires sites at nine points: three, each separated by 1 km, along each of three narrow and lightly-used dirt roads. Counts at the Tortolita Mountains site consisted of either five individual points or two sets of three points; in both cases points were separated by 1 km or more (logistics at Tortolita required two separate routes).

Calling poorwills were counted at each point for 3 min during which time CPW, who conducted all counts, remained in darkness and silent (playbacks of poorwill calls were not used). The number of calling birds was assigned based on differing direction and distance of calls and temporal overlap in calling

(i.e., 2 or more birds calling at the same time). Counts were started at least 1 hr after sunset and completed in 1–2 hrs. No counts were conducted during civil twilight (when the sun is 0° to 6° below the horizon), even though poorwills called frequently during this time, so that solar light did not complicate our interpretation of the influence of lunar illumination. No counts were conducted when it rained.

We recorded environmental variables twice (Tortolita Mountains) or three (Research Ranch and Buenos Aires) times during each survey, and averaged them to establish overall count conditions. We measured ambient light levels, temperature, relative humidity, average wind speed, and percent cloud cover. Wind speed and/or relative humidity were not measured during 49 counts. A Beseler PM2L Color Analyzer (Charles Beseler Co., Linden, NJ, USA) was used to measure ambient light levels (Hecker and Brigham 1999). This device generates a unit-less measure of light intensity to facilitate setting exposure times for film printing. It works at light intensities at which many light meters are ineffective. We used a Cole-Parmer thermistor thermometer (Model 8402-00; Cole-Parmer Instrument Co., Vernon Hills, IL, USA) to measure ambient temperature and a General Eastern thermo-hygrometer (Model 880, General Eastern Instruments, Woburn, MA, USA) to measure relative humidity. We measured wind speed (± 3 km/hr) over a 3–4 min period with a Kestrel wind meter (NK Electronics, Chester, PA, USA), which averaged measurements taken at 1-sec intervals. Percent cloud cover was visually estimated.

Most birds called during the warmer months and we included for our analysis the 92 counts between 5 May and 3 September, during which time 80% of all calling occurred. Forty-seven of the 92 counts included in our analysis were at the Research Ranch, 42 at Buenos Aires, and 3 at Tortolita Mountains. We assumed there was no site specific lunar effect. The maximum number of birds heard at each point along each route within any year was used as an estimate of year- and site-specific bird maximums. The number of calls detected during any count were standardized against the maximums and our analysis was based on the percentage of the maximum number of birds calling, not the number of birds specifically. We used two separate backward stepwise multiple regressions to assess the importance of environmental variables. First, for all 92 counts with light, temperature, and percent cloud cover as variables, and second, for the smaller sample of 43 counts for which data on relative humidity and wind speed were also available.

Influence of Owls on Vocalization.—We assessed the influence of owls on calling behavior by poorwills by measuring the response to playbacks of poorwill calls both with and without the implied presence of a Great Horned Owl (these owls are common nocturnal predators and were heard in all 3 study areas). We surveyed for calling poorwills (independently from the counts described) using two playback treatments to discern the effect of potential owl presence on poorwill calling behavior under differing light levels. Playbacks were conducted at 1.6-km intervals on dirt road systems at the Research Ranch and Tortolita Mountains sites, as well as on lightly traveled dirt roads on the east side of the Rincon Mountains, 50 km east of Tucson (32° 07′ N, 110° 28′ W), on desert flats near Black Mountain, 60 km north of Tucson (32° 49′ N, 110° 57′ W), and on the west side of the Silverbell Mountains, 55 km west of Tucson (32° 26′ N, 111° 30′ W). At each stop, we waited in silence and darkness for 30 sec and then played a treatment tape. The test was conducted between 6 June and 11 July 1998 on calm or nearly calm nights with little or no cloud cover, beginning at least 90 min after sunset. The test usually took several hours and was not repeated on the same evening. Three routes were surveyed twice, once during the full moon and again during no moon, and two were surveyed three times each, twice during a full moon (separated temporally by 1 month) and once when there was no moon.

We randomly assigned a treatment to each stop prior to surveys, but with the condition that each set of two stops included each treatment. Counts were based on response to two playbacks treatments: poorwill only (15 sec poorwill, 60 sec silence, 15 sec poorwill) and poorwill, Great Horned Owl, poorwill (15 sec poorwill, 60 sec silence, 15 sec Great Horned Owl, 15 sec poorwill). The treatment variation thus occurred in the second call sequence. Re-

cordings used in treatments were taken from a standard collection of bird songs (Peterson Field Guides: Western Bird Songs, Houghton Mifflin Co., Boston, MA, USA). Complete 90–120 sec treatment tapes were created so that switching of tapes during counts was unnecessary. We used a portable cassette player, set at 3/4 maximum volume and judged that poorwills within ~300 m responded.

We measured the number of responding birds and calling intensity during the 60-sec interval following playback of the initial call and again during the 60-sec interval following playback of the treatment call(s). The number of birds calling was based on the direction and distance of calls, and overlap in calling. To characterize intensity, we counted the total number of calls, regardless of the number of birds calling, and assigned a categorical value based on six categories: (0) no calls, (1) 1–5 calls, (2) 6–10 calls, (3) 11–20 calls, (4) 21–30 calls, and (5) 31+ calls. Categorical values were used to minimize potential errors in counting when calling was particularly intense. We completed 12 surveys with a total of 168 individual stops, 84 for each treatment. Stops at which no poorwills were heard (29 in total), were eliminated from our analysis. We initially compared the full versus new moon results prior to the treatment playback (i.e., the numerical and categorical response to the first poorwill call only). A subsequent analysis to assess treatment effects was based on the per point change in number of birds or calls from the 60-sec period after the first playback to the 60-sec period after the second playback. Preliminary analysis indicated that data for both survey treatments were not normally distributed (Shapiro-Wilks' W with associated $P < 0.01$); therefore, we used a nonparametric Mann-Whitney U-test for all comparisons.

RESULTS

Likelihood of Activity.—We used data from 135 activity records (59 full moon, 76 new moon) for the period 1 hr past sunset, 112 (56 full moon, 56 new moon) for 3 hrs past sunset, and 97 (48 full moon, 49 new moon) for 5 hrs past sunset to examine poorwill movements. The likelihood that a bird was active during full moon was similar in the three time periods with movement occurring in 70% (1 hr), 61% (3 hrs), and 69% (5 hrs) of each. The likelihood of activity decreased over time during the new moon with movements occurring in 86, 39, and 25% of the three periods, respectively (Fig. 1). Birds were more likely to be active 3 and 5 hrs past sunset when the moon was full versus when it was new ($\chi^2_1 = 5.1$, $P = 0.023$ and $\chi^2_1 = 19.1$, $P < 0.001$, respectively). The situation was reversed, however, 1 hr past sunset, when activity was more common during the new than the full moon ($\chi^2_1 = 5.1$, $P = 0.024$).

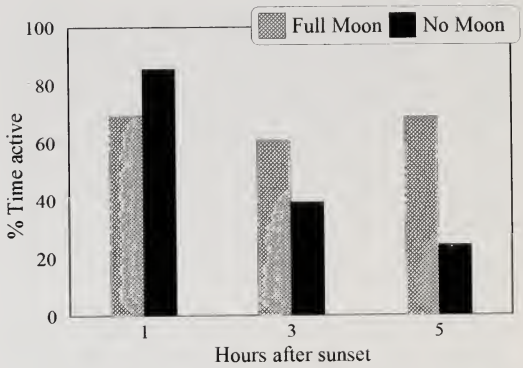


FIG. 1. Likelihood of activity by Common Poorwills during 5-min periods 1, 3, and 5 hrs after sunset in southern Arizona. There were between 97 and 135 sampling periods within each time period, and activity differs within each (χ^2 tests, all $P < 0.05$).

Environmental Influences on Vocalizations.—Poorwills in southern Arizona called throughout an extended period from March through October (Fig. 2). Most calling occurred during the summer months. The central 50 and 80% of all calls were recorded between 27 May and 29 July, and 5 May and 9 September, respectively. Ambient light levels significantly predicted poorwill calling, whether based on the data from 92 counts for which only light, temperature, and cloud cover were analyzed ($F_{1,89} = 92.2$, $R^2 = 0.509$, $P < 0.001$, $\beta_{Light} = 0.71$; Fig. 3), or based on the data from 43 counts that also included relative humidity and wind speed ($F_{1,41} = 49.1$, $R^2 = 0.545$, $P < 0.001$, $\beta_{Light} = 0.74$). No other environmental variable measured was significantly related to the number of calling birds, regardless of the data set used.

Influence of Owls on Vocalizations.—The effect of moonlight on calling was also evident from playback surveys whose purpose

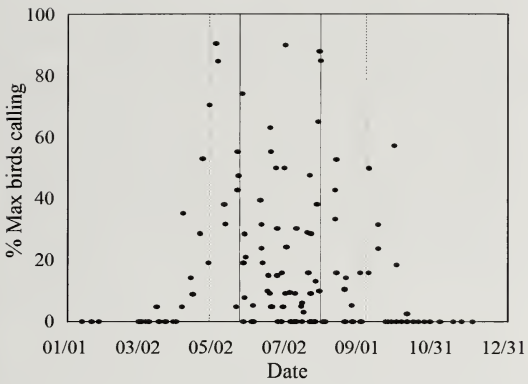


FIG. 2. Seasonality of calling by Common Poorwills in southern Arizona from point count surveys without playback of a poorwill call. Solid lines encompass the central 50% of all calls, and stippled lines the central 80%.

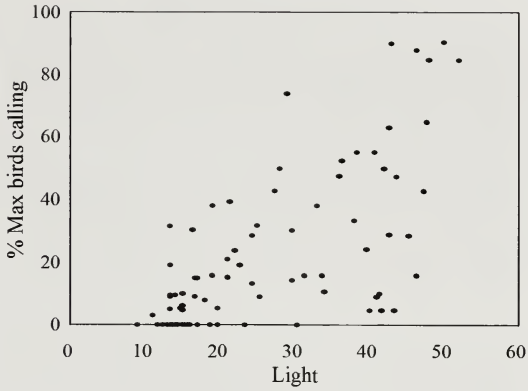


FIG. 3. Relationship between ambient light at night and calling by Common Poorwills during spring and summer in southern Arizona without playback of a poorwill call. Light levels are unit-less measurements from a photographic light meter, with "10" representative of no moon and little light, and "50" of a full moon and bright conditions.

was to evaluate the effect of owl calls on poorwill vocalizing. Poorwills responded in significantly greater numbers and more intensely during full moons versus new moons after playback of the first poorwill call. The number of birds responding during the new moon averaged only 38% of the number calling during the full moon (mean of 0.59 birds at each point vs. 1.55 birds; $Z_{54,85} = 5.66$, $P < 0.001$). The categorical number of calls detected during the new moon averaged 52% of the number heard during full moon (1.57 vs. 3.02; $Z_{54,85} = 4.51$, $P < 0.001$).

There was no significant difference in the change in calling response following playback of the second treatment call(s) during the full moon either in number of birds responding or intensity of calling. The number of responding poorwills increased 16% (from 1.64 to 1.90 birds) per point following the poorwill only treatment during the full moon from the period after the first call to the period after the second. Calling increased 14% (from 1.47 to 1.67 birds) after the Great Horned Owl then poorwill treatment ($Z_{42,43} = 0.14$, $P > 0.1$). The number of calls increased 21% (from 3.05 to 3.69) after the poorwill only treatment, and 11% (from 3.00 to 3.33) following the Great Horned Owl then poorwill treatment ($Z_{42,43} = 0.85$, $P > 0.1$). In contrast, there was a significant difference in the change in response by poorwills when the moon was new, both in the number of birds responding and the categorical intensity of calling. The number of responding poorwills following the poorwill only treatment during the new moon increased 59% (from 0.56 to 0.89 birds) after the second call compared to after the first call, but decreased 11% (from 0.63 to 0.56 birds) after the Great Horned Owl then poorwill treatment ($Z_{27,27} = 2.42$, $P = 0.016$). Categorically, the number of calls increased 35% (from 1.59 to 2.15) after the poorwill only treatment, but decreased 4% (from 1.56 to 1.48) following the Great Horned Owl then poorwill treatment ($Z_{27,27} = 2.19$, $P = 0.029$).

DISCUSSION

The intensity of night-time lunar illumination varies by more than a hundred-fold depending on phase (Austin et al. 1976). Consequently, it is not surprising that lunar phase should influence behavior of nocturnal animals, especially those that orient visually, although the direction of this influence may not be obvious. In the absence of extenuating factors, visually-oriented nocturnal predators like poorwills should concentrate foraging activity during bright moonlight but vocalize more frequently when there is little moonlight, when foraging should be least efficient (Brigham and Barclay 1992, Csada et al. 1992, Bayne and Brigham 1995). Chuck-will's-widows (*Caprimulgus carolinensis*) and Whip-poor-wills (*C. vociferus*) call with greater frequency during moonlit conditions, how-

ever, and lunar illumination is the only environmental factor correlated with calling during the breeding season (Cooper 1981, Mills 1986, Ganey 1990). Poorwills in our study vocalized most actively during the full moon and lunar illumination was the only environmental variable we measured with which the number of birds heard calling was correlated. In addition, poorwills tended to be more active (which we interpret as foraging) during full moon, although the number of flying insect prey depended principally on temperature and was independent of ambient light (Woods 2002). Consequently, increased activity by poorwills during the brightest periods was not related to increased prey density, and vice versa.

Jetz et al. (2003) found a strong relationship between lunar cycle and timing of foraging activity by Standard-winged (*Macrodipteryx longipennis*) and Long-tailed (*Caprimulgus climacurus*) nightjars in equatorial West Africa. They noted that foraging was concentrated during the crepuscular period during all phases of the lunar cycle but increased significantly around new moon. They also detected a small but significant increase in abundance of some larger insects during full moon periods which correlated with increased foraging during periods of the night with lunar light. In cooler more seasonal subtropical environments, temperature as well as light levels strongly affects activity patterns of Freckled Nightjars (*Caprimulgus tristigma*; R. A. M. Ashdown and A. E. McKechnie, unpubl. data). Unfortunately, calling behavior was not evaluated in either of these studies.

Peaks in calling occur for some nocturnal birds throughout the breeding season, and are often attributed to different breeding stages (e.g., Clark and Anderson 1997). We found no seasonal peaks in calling, possibly because of the cyclic influence of lunar phase on calling frequency. Poorwills are known to call persistently (Bent 1940, Gabrielson and Jewett 1940, Bailey and Niedrach 1965, this study), and we heard birds call in every month but January. These observations support the hypothesis that individuals are inclined to call frequently where they occur as year-round residents, regardless of breeding stage, but in locations where they are migratory, calling tends to cease in late summer (Kalcounis et al. 1992). These results suggest a trade-off exists between frequent calling and efficient foraging, assuming that calling reduces foraging efficiency. The extent to which vocalizing may restrict foraging by caprimulgids is uncertain, but males deplete fat reserves during the breeding season whereas females, which probably call infrequently, do not (Csada and Brigham 1992, Thomas et al. 1996). Energetic shortfalls resulting from forgoing feeding when prey are most visible are probably minimized since full moons are above the horizon for the most time. Consequently, more foraging time is available when the moon is relatively full. During new moon, activity was highest shortly after sunset and diminished as evening progressed, whereas during full moon, activity levels were consistent throughout late evening (cf. Brauner 1952). These contrasting patterns suggest that during new moons, poorwills must forage with greater intensity at and just past twilight, since low light levels will reduce foraging efficiency and may increase predation risk later in the night.

Why are poorwills more vocal during periods of high lunar illumination? In addition to the offsetting increase in time available for foraging, the ease with which males can move within and defend their territories is likely enhanced by relatively bright conditions. Our results suggest the ability to detect and evade predators is also important when calling advertises location. This explanation is supported by the higher intensity of calling in response to conspecific calls following owl playbacks during the full moon, but an apparent reluctance to respond under similar circumstances during the new moon. Other relatively small nocturnal birds that are especially vocal when the moon is bright also have acute vision and rely heavily on vision to forage (e.g., Whip-poor-will). We surmise that visual acuity influences timing or extent to which smaller nocturnal animals vocalize at night. For nocturnal animals that may less easily detect and out-maneuver predators, the increased risk of predation during the full moon selects for less activity. Gerbils (*Gerbillus* spp.) and other desert rodents, as well as Australian Owlet-Nightjars (*Aegotheles cristatus*), adjust foraging patterns to avoid bright moonlight and are all preyed upon by owls (Price et al. 1984, Brown et al. 1988, Kotler et al.

1994, Brigham et al. 1999). Notably, one male radio-marked poorwill was killed by an owl (*Otus* sp.) in our study. The bird was taken under relatively dim conditions when the moon was in its first quarter and setting. Whether specific predators and or predator foraging strategies are the major selective pressures which have shaped the differences in response to lunar conditions between caprimulgids and some rodents, remains to be understood.

Future research is needed with an emphasis on explaining the role of lunar illumination on behavior of other birds that are active at night, including those that are generally considered diurnal (e.g., Johnson et al. 2003). The lunar cycle is relatively short in comparison with the overall breeding season for most birds, and consideration of this variable could provide insight into foraging strategies and timing of breeding. Knowledge of the lunar phase and its effect on both foraging by and predation risk on nocturnal birds may also be an important consideration for surveying nocturnal species (Ganey 1990, Downs 1998). Additionally, our study sites were relatively distant from large urban centers and the light pollution associated with them. Light pollution could relieve some dependence on moonlight for efficient foraging by predators but, as a consequence, enhance predation pressure on their prey (Buchanan 2005, Frank 2005, Lloyd 2005). Perhaps more importantly, the loss of cyclic variation in nocturnal illumination may disrupt behaviors that evolved in association with regular fluctuation between bright and dark periods (Rich and Longcore 2005). Additional research into the impact of light pollution on the behavior of nocturnal animals is essential, considering the extent to which it has altered the night sky in many developed regions.

ACKNOWLEDGMENTS

P. A. Bradshaw, R. K. Sechler, and B. A. Woods assisted in trapping and radio-marking poorwills. The National Audubon Society and W. V. Branan provided generous access to the Appleton-Whittell Research Ranch and logistic support. Comments by C. E. Braun and two anonymous reviewers greatly improved the manuscript. Funding for this research was provided in part by awards to CPW from the Faculty of Graduate Studies and Research at the University of Regina and an NSERC research grant to RMB.

LITERATURE CITED

Austin, R. H., B. F. Phillips, and D. J. Webb. 1976. A method for calculating moonlight illuminance at the earth's surface. Journal of Applied Ecology 13:741–748.

Bailey, A. M. and R. J. Niedrach. 1965. Birds of Colorado. Denver Museum of Natural History, Denver, Colorado, USA.

Bayne, E. M. and R. M. Brigham. 1995. Prey selection and foraging constraints in Common Poorwills (*Phalaenoptilus nuttallii*: Aves: Caprimulgidae). Journal of Zoology 235:1–8.

Beier, P. 2005. Effects of artificial night lighting on terrestrial mammals. Pages 19–42 *in* Ecological consequences of artificial night lighting (C. Rich and T. Longcore, Editors). Island Press, Washington, D.C., USA.

Bent, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U.S. National Museum Bulletin 176.

Brauner, J. 1952. Reactions of poor-wills to light and temperature. Condor 54:152–159.

Brigham, R. M. 1992. Daily torpor in a free-ranging goatsucker, the Common Poorwill (*Phalaenoptilus nuttallii*). Physiological Zoology 65:457–472.

Brigham, R. M. and R. M. R. Barclay. 1992. Lunar influence on foraging and nesting activity of Common Poorwills (*Phalaenoptilus nuttallii*). Auk 109:315–320.

Brigham, R. M., R. C. A. Gutsell, R. S. Wiacek, and F. Geiser. 1999. Foraging behaviour in relation to the lunar cycle by Australian Owlet-Nightjars *Aegotheles cristatus*. Emu 99:253–261.

Brooke, M. 1990. The Manx Shearwater. T. & A. D. Poyser, London, United Kingdom.

Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76:408–415.

Buchanan, B. W. 2005. Observed and potential effects of artificial night lighting on anuran amphibians. Pages 192–220 *in* Ecological consequences of artificial night lighting (C. Rich and T. Longcore, Editors). Island Press, Washington, D.C., USA.

Clark, K. A. and S. H. Anderson. 1997. Temporal, climatic and lunar factors affecting owl vocalizations of western Wyoming. Journal of Raptor Research 31:358–363.

Cooper, R. J. 1981. Relative abundance of Georgia caprimulgids based on call-counts. Wilson Bulletin 93:363–371.

Csada, R. D. and R. M. Brigham. 1992. Common Poorwill (*Phalaenoptilus nuttallii*). The birds of North America. Number 32.

Csada, R. D., R. M. Brigham, and B. R. Pittendrigh. 1992. Prey selection in relation to insect availability by the Common Poorwill (*Phalaenoptilus nuttallii*). Canadian Journal of Zoology 70:1299–1303.

Downs, K. D. 1998. Common Snipe surveys, habitat

and evaluation of the Breeding Bird Survey. Thesis. University of Wyoming, Laramie, USA.

Frank, K. D. 2005. Effects of artificial night lighting on moths. Pages 305–344 *in* Ecological consequences of artificial night lighting (C. Rich and T. Longcore, Editors). Island Press, Washington, D.C., USA.

Gabrielson, I. N. and S. G. Jewett. 1940. Birds of Oregon. Oregon State Monographs 2. Oregon State College, Corvallis, USA.

Ganey, J. L. 1990. Calling behavior of Spotted Owls in northern Arizona. Condor 92:485–490.

Hecker, K. R. and R. M. Brigham. 1999. Does moonlight change vertical stratification of activity by forest dwelling insectivorous bats? Journal of Mammalogy 80:1196–1201.

Hill, I. F., B. H. Cresswell, and R. E. Kenward. 1999. Field-testing the suitability of a new backpack harness for radio-tagging passerines. Journal of Avian Biology 30:135–142.

Jackson, H. D. 1984. Finding and trapping nightjars. Bokmakierie 36:86–89.

Jackson, H. D. 1985. Aspects of the breeding biology of the Fierynecked Nightjar. Ostrich 56:263–276.

Jetz, W., J. Steffen, and K. E. Linsenmair. 2003. Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars. Oikos 103:627–639.

Johnson, M., J. P. Beckmann, and L. W. Oring. 2003. Diurnal and nocturnal behavior of breeding American Avocets. Wilson Bulletin 115:176–185.

Kalcounis, M. C., R. D. Csada, and R. M. Brigham. 1992. The status and distribution of the Common Poorwill in the Cypress Hills, Saskatchewan. Blue Jay 50:38–44.

Keitt, B. S., B. R. Tershy, and D. A. Croll. 2004. Nocturnal behavior reduces predation pressure on Black-vented Shearwaters *Puffinus opisthomelas*. Marine Ornithology 32:173–178.

Kotler, B. P., Y. Ayal, and A. Subach. 1994. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. Oecologia 100:391–396.

Lang, A. B., E. K. V. Kalko, H. Römer, C. Bockholdt, and D. K. N. Dechmann. 2006. Activity levels of bats and katydids in relation to the lunar cycle. Oecologia 146:659–666.

Lloyd, J. E. 2005. Stray light, fireflies, and fireflyers. Pages 345–364 *in* Ecological consequences of artificial night lighting (C. Rich and T. Longcore, Editors). Island Press, Washington, D.C., USA.

Mills, A. M. 1986. The influence of moonlight on the behavior of goatsuckers (Caprimulgidae). Auk 103:370–378.

Nelson, D. A. 1989. Gull predation on Cassin's Auklet varies with lunar cycle. Auk 106:495–497.

Perrins, C. M. and H. Q. P. Crick. 1996. Influence of lunar cycle on laying dates of European Nightjars (*Caprimulgus europaeus*). Auk 113:705–708.

Price, M. J., N. W. Waser, and T. A. Bass. 1984. Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65:211–219.

Rich, C. and T. Longcore (Editors). 2005. Ecological consequences of artificial night lighting. Island Press, Washington, D.C., USA.

Sutter, G. C., D. J. Sawatzky, D. M. Cooper, and R. M. Brigham. 1996. Renesting intervals in Sprague's Pipit, *Anthus spragueii*. Canadian Field-Naturalist 110:694–697.

Swenson, J. E. and S. Swenson. 1977. Nightlighting as a method for capturing Common Nighthawks and other caprimulgids. Bird Banding 48:279–280.

Thomas, D. W., R. M. Brigham, and H. Lapierre. 1996. Field metabolic rates and body mass changes in Common Poorwills (*Phalaenoptilus nuttallii*: Caprimulgidae). Ecoscience 3:70–74.

Woods, C. P. 2002. Ecological aspects of torpor use and inactivity during winter by Common Poorwills. Dissertation. University of Regina, Regina, Saskatchewan, Canada.

The Wilson Journal of Ornithology 120(3):513–518, 2008

MAXIMIZING DETECTION PROBABILITY OF WETLAND-DEPENDENT BIRDS DURING POINT-COUNT SURVEYS IN NORTHWESTERN FLORIDA

CHRISTOPHER P. NADEAU,[1,3] COURTNEY J. CONWAY,[1] BRADLEY S. SMITH,[1] AND THOMAS E. LEWIS[2]

ABSTRACT.—We conducted 262 call-broadcast point-count surveys (1–6 replicate surveys on each of 62 points) using standardized North American Marsh Bird Monitoring Protocols between 31 May and 7 July 2006 on St. Vincent National Wildlife Refuge, an island off the northwest coast of Florida. We conducted double-blind multiple-observer surveys, paired morning and evening surveys, and paired morning and night surveys to examine the influence of call-broadcast and time of day on detection probability. Observer detection probability for all species pooled was 75% and was similar between passive (69%) and call-broadcast (65%) periods. Detection probability was higher on morning than evening (t = 3.0, P = 0.030) or night (t = 3.4, P = 0.042) surveys when we pooled all species. Detection probability was higher (but not significant for all species) on morning compared to evening or night surveys for all five focal species detected on surveys: Least Bittern (*Ixobrychus exilis*), Clapper Rail (*Rallus longirostris*), Purple Gallinule (*Porphyrula martinica*), Common Moorhen (*Gallinula chloropus*), and American Coot (*Fulica americana*). We detected more Least Bitterns (t = 2.4, P = 0.064) and Common Moorhens (t = 2.8, P = 0.026) on morning than evening surveys, and more Clapper Rails (t = 5.1, P = 0.014) on morning than night surveys. *Received 2 March 2007. Accepted 6 October 2007.*

Maximizing detection probability of rare or inconspicuous birds during point-count surveys is essential so that sufficient individuals are detected to reliably estimate population trends (Lynch 1995). Wetland-dependent birds (i.e., rails and bitterns) are among the most inconspicuous groups of birds in North America. They vocalize infrequently and often occur in isolated wetlands making them difficult to monitor (Bystrak 1981, Gibbs and Melvin 1993). A marsh bird monitoring protocol was developed in 1999 for conducting standardized surveys for wetland-dependent birds across North America (Conway 2007). The protocol instructs surveyors to use call-broadcast after an initial 5-min passive period to increase vocalization probability of birds present during the survey period. However, call-broadcast might interfere with the observer's ability to hear vocalizing birds during the survey (Conway and Nadeau 2006). A decrease in observer detection probability could potentially negate the benefits of increased vocalization probability. Few studies have examined the effects of call-broadcast on observer detection probability and participants using this protocol are not obligated to use methods (i.e., multiple-observer surveys) to account for variation among observers.

Vocalization probability of wetland-dependent birds varies with time of day and diurnal patterns may vary regionally and among species (Conway and Gibbs 2001). Thus, surveyors should identify the optimal time of day to conduct surveys in their region to maximize detection probability. The Standardized North American Marsh Bird Monitoring Protocol (Conway 2007) instructs participants to conduct surveys in the morning or evening when birds are most vocal. Participants using the protocol are not obligated to define which of the two daily time periods is optimal in their region and few participants have attempted to do so. Many species of wetland-dependent birds are known to vocalize at night (e.g., Black Rail [*Laterallus jamaicensis*], Clapper Rail [*Rallus longirostris*], Virginia Rail [*R. limicola*], Yellow Rail [*Coturnicops noveboracensis*], and American Bittern [*Botaurus lentiginosus*]; Reynard 1974, Meanley 1985, Johnson and Dinsmore 1986, Gibbs et al. 1992, Bookhout 1995), yet few studies have attempted to examine the efficacy of night surveys. We compared morning to evening sur-

[1] USGS, Arizona Cooperative Fish and Wildlife Research Unit, 325 Biological Sciences East, University of Arizona, Tucson, AZ 85721, USA.

[2] St. Vincent National Wildlife Refuge, U.S. Fish and Wildlife Service, 479 Market Street, P. O. Box 447, Apalachicola, FL 32329, USA.

[3] Corresponding author;
e-mail: cnadeau@email.arizona.edu

veys and morning to night surveys to ascertain the optimal time of day to conduct surveys for wetland-dependent birds in the southeastern United States. Our specific objectives were to: (1) compare observer detection probability between passive and call-broadcast surveys in the context of the North American Marsh Bird Monitoring Protocol, and (2) ascertain the optimal time of day to conduct surveys for wetland-dependent birds in the southeastern United States.

METHODS

Study Area.—All surveys were conducted on the St. Vincent Island (SVI) portion of St. Vincent National Wildlife Refuge (29° 40′ N, 85° 05′ W). SVI is a 4,968 ha forested barrier island in the northeastern Gulf of Mexico bounded by St. Vincent Sound, Apalachicola Bay, and the Gulf of Mexico. Thirty-seven percent of the island is considered suitable habitat for wetland-dependent birds: 308 ha of managed marsh, 67 ha of managed open water, 1,090 ha of estuarine marsh, and 383 ha of estuarine open water (Grace 2000). Palustrine marsh (270 ha) and palustrine scrub (43 ha) wetlands exist on the island, but were not surveyed since few wetland-dependent birds have been detected in these wetland types. We established five survey routes on SVI: three were in managed marshes and two were in estuarine marshes. Vegetation on three survey routes was dominated by *Cladium*. The other two routes were co-dominated by *Typha* and *Juncus* or *Spartina* and *Cladium*. Salinity in the managed marshes increased throughout the study and ranged from 3.1 to 18.5 ppt. Salinity measurements were not available for the estuarine marshes. We established 62 survey points, placing 12–14 points on each survey route. Adjacent points were spaced 200 m apart (400 m on one route to conform to past surveys). We chose an interval of 200 m on the four newly established routes to increase our probability of detecting Black Rails, which are rarely detected beyond 100 m (Conway et al. 2004). Survey points were marked in the field with a portable GPS receiver and with rebar or surveyor tape.

Surveys.—Survey methods followed the Standardized North American Marsh Bird Monitoring Protocol (Conway 2007). We recorded all aural and visual detections of 10 focal species during each minute of both a 5-min passive listening period and a 5-min call-broadcast period at each point. The 10 focal species thought to occur in the area included Pied-billed Grebe (*Podilymbus podiceps*), Least Bittern (*Ixobrychus exilis*), American Bittern, Black Rail, Clapper Rail, King Rail (*Rallus elegans*), Sora (*Porzana carolina*), Purple Gallinule (*Porphyrula martinica*). Common Moorhen (*Gallinula chloropus*), and American Coot (*Fulica americana*). The call-broadcast period was composed of 30 sec of broadcast calls followed by 30 sec of silence for each of five species in the following sequence: Black Rail, Least Bittern, Clapper Rail, Common Moorhen, and Purple Gallinule. We used the standardized call-broadcast recordings for the North American Marsh Bird Monitoring Protocol (Conway 2007) that we obtained from the coordinators of the program. We did not broadcast for all (5 of 10) focal species to limit the duration of the survey at each point. We excluded species of lesser management concern or species commonly detected without the use of call-broadcast. We excluded King Rail from our call-broadcast due to the similarity between King Rail and Clapper Rail calls and because they commonly respond to each others' calls (Conway and Nadeau 2006). Surveys were conducted on days without rain and when winds were <10 km/hr. All calls were broadcast using a Memorex CD player (Model #MD6443SIL) and a Sony SRS-A27 Active Speaker System placed on the ground or bow of the canoe pointed perpendicular to the edge of the marsh. All broadcasts were ~90 dB measured 1 m from the speaker. We used a Kestrel 3000 weather anemometer to record temperature and wind speed at the beginning and end of each survey route. We also estimated percent cloud cover at the beginning and end of each survey route. We measured temperature, wind speed, and cloud cover to examine whether differences in detection probability during different periods (morning, evening, and night) were potentially due to differences in weather conditions.

Double-blind Multiple-observer Surveys.—We conducted double-blind multiple-observer surveys at 26 points on two survey routes on 25 June and 5 July 2006. Double-observer surveys require two trained observers. We only had two trained observers and chose each

route based on the route observer #1 planned to survey (for the second part of our study) on the day observer #2 was available. Both observers estimated the distance to each bird detected and recorded the call given by each bird. We were able to use these auxiliary data to easily identify (after the survey) which birds had and had not been detected by each observer. The two observers stood side-by-side or sat on opposite ends of a canoe during the surveys. They recorded their data inconspicuously during the survey, by recording their data discreetly and by shielding their data sheets with their clipboard, to not alert the other observer when they detected a bird. They did not discuss their detections until the survey was complete.

We followed Nichols et al. (2000) to estimate observer detection probability for each of two observers (P_1 and P_2) during each of three time periods: (1) the entire survey (passive and call-broadcast combined), (2) the passive period only, and (3) the call-broadcast period only. We averaged P_1 and P_2 to obtain an overall estimate of observer detection probability for each of the three time periods.

Detection Probability During Different Times of Day.—We conducted 144 paired point-count surveys on three survey routes (38 points with 2–6 replicates/point) during both the morning and evening. Paired surveys were conducted on the same day or consecutive days between 31 May and 30 June 2006. Morning surveys were conducted 0.5 hrs before sunrise until no later than 1000 hrs EDT, and evening surveys were conducted 3 hrs before sunset until dark. We also conducted 104 paired point-count surveys on two different routes (26 points with 4 replicates per point) during both the morning and night. Paired surveys were conducted on the same day or consecutive days between 7 June and 7 July 2006. Morning surveys were conducted 0.5 hrs before sunrise until no later than 1000 hrs, and night surveys were conducted between 0100 and 0400 hrs. Paired morning versus evening surveys were conducted on different survey routes than paired morning versus night surveys with the exception of one pair of surveys.

We used paired *t*-tests to compare the mean number of wetland-dependent birds detected (all species pooled) and the mean number of each species detected on each route between morning and evening surveys, and between morning and night surveys. We also used paired *t*-tests to compare temperature, wind speed, and percent cloud cover between morning and evening surveys, and between morning and night surveys.

RESULTS

Double-blind Multiple-observer Surveys.—We detected 5 of 10 focal species during double-blind multiple-observer surveys: Least Bittern, American Bittern, Clapper Rail, King Rail, and Common Moorhen. Observer detection probability for all species pooled across the entire survey (passive and call-broadcast periods combined) was 75%. The observer detection probability was similar for both the passive period (69%) and call-broadcast period (65%).

Detection Probability During Different Times of Day.—We detected 5 of 10 focal species on at least one of the 12 paired morning and evening surveys: Least Bittern, Clapper Rail, Purple Gallinule, Common Moorhen, and American Coot. The mean (± SE) number of birds detected was higher ($t = 3.0$, $P = 0.030$) on morning ($\bar{x} = 19.8 \pm 6.5$ birds) than on evening surveys ($\bar{x} = 7.8 \pm 3.3$ birds) when we pooled all species. We detected 106% more Least Bitterns ($t = 2.4$, $P = 0.064$) and 170% more Common Moorhens ($t = 2.8$, $P = 0.026$) on morning than on evening surveys (Fig. 1A). We did not observe significant differences in the number of individuals detected between morning and evening surveys for Clapper Rail, Purple Gallinule, and American Coot. We did not observe a difference in percent cloud cover ($t = 0.8$, $P = 0.31$) or wind speed ($t = 0$, $P = 1.00$) between morning ($\bar{x}_{cloud} = 19 \pm 7\%$, $\bar{x}_{wind} = 1.5 \pm 0.1$ km/hr) and evening ($\bar{x}_{cloud} = 22 \pm 8\%$, $\bar{x}_{wind} = 1.5 \pm 0.3$ km/hr) surveys, but temperature was 8% higher on evening ($\bar{x}_{temp} = 28.6 \pm 0.5°$ C) than on morning ($\bar{x}_{temp} = 26.6 \pm 0.8°$ C) surveys ($t = 3.5$, $P = 0.017$).

We detected 3 of 10 focal species on at least one of the eight paired morning and night surveys: Least Bittern, Clapper Rail, and Common Moorhen. The mean number of birds detected was higher ($t = 3.4$, $P = 0.042$) on morning ($\bar{x} = 5.5 \pm 1.7$ birds) than on night surveys ($\bar{x} = 1.2 \pm 0.6$ birds) when we pooled

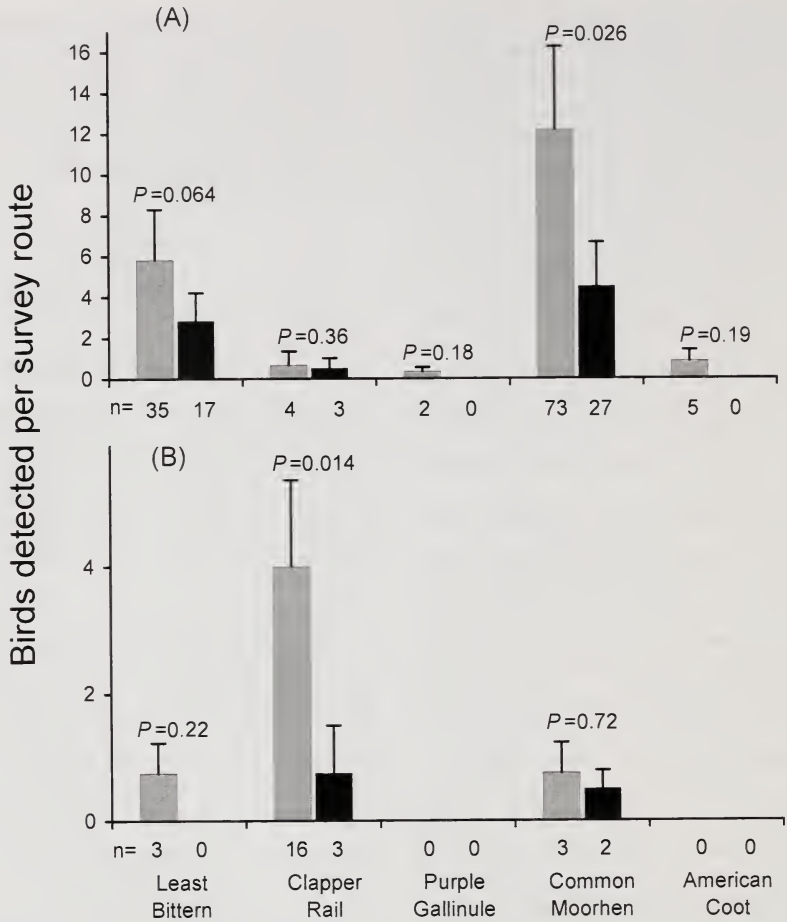


FIG. 1. Mean (± SE) number of wetland-dependent birds detected during (A) six morning (gray) and six evening (black) surveys, and (B) four morning (gray) and four night (black) surveys on St. Vincent National Wildlife Refuge, northwestern Florida, 31 May–7 July 2006. Data in (A) and (B) were from different survey routes and can not be appropriately compared. Sample sizes (*n*) refer to the total number of birds detected.

all species. We detected 433% more Clapper Rails (t = 5.1, P = 0.014) on morning than on night surveys (Fig. 1B). We did not observe significant differences in number of individuals detected between morning and night surveys for Least Bittern or Common Moorhen. We did not observe a difference in temperature (t = 0.3, P = 0.76) between morning ($\bar{x}_{temp}$ = 25.4 ± 0.7° C) and night ($\bar{x}_{temp}$ = 25.1 ± 1.3° C) surveys. Percent cloud cover (t = 2.3, P = 0.10) and wind speed (t = 2.8, P = 0.066) were higher on morning ($\bar{x}_{cloud}$ = 39 ± 17%, $\bar{x}_{wind}$ = 2.4 ± 0.3 km/hr) than on night ($\bar{x}_{cloud}$ = 23 ± 21%, $\bar{x}_{wind}$ = 0.8 ± 0.5 km/hr) surveys, however, the differences were only marginally significant.

DISCUSSION

Our results suggest that call-broadcast has little or no negative effect on observer detection probability. These results support use of call-broadcast to maximize detection probability during wetland-dependent bird surveys. Other studies have shown that observer detection probability is higher during the call-broadcast period for Clapper Rails and similar between passive and call-broadcast periods for all other species (Conway and Nadeau 2006). We observed similar patterns although our sample sizes for individual species were small. Our estimate of observer detection probability (75%) is similar to previous esti-

mates (50–75%) for wetland-dependent birds (Conway et al. 2004, Conway and Nadeau 2006). Our results suggest that trained observers are missing 25% of the birds vocalizing during a survey that combines both passive and call-broadcast methodology. Thus, accounting for detection probability during surveys is essential if data will be used to estimate a measure of true abundance. Moreover, our individual estimates of observer detection probability (68 and 82%) differed between our two trained observers. Hence, estimating observer detection probability for each observer is important if data from multiple observers will be used to estimate population trends over time.

We detected more birds on morning surveys compared to both night and evening surveys for all species detected. Higher temperatures in the evening may explain the decrease in the number of wetland-dependent birds detected between morning and evening surveys. Past studies examining the effects of temperature on the detection probability of wetland-dependent birds have reported conflicting results. Previous studies have reported a positive correlation between temperature and detection probability (e.g., Mangold 1974, Tacha 1975, Spear et al. 1999) and others have shown a negative correlation (e.g., Tango et al. 1997). However, authors of these studies failed to account for the correlation between temperature and time of day or time of year (Conway and Gibbs 2001). Future studies that examine how weather affects detection probability need to first control for time of day. Robbins (1981) suggested that extreme heat reduces bird activity in other groups of birds. Higher wind speeds and percent cloud cover in the morning did not make morning less effective than night surveys. Robbins (1981) also reported two peak singing periods for birds (one in the morning and one in the evening) but the peak singing period in the morning was substantially longer. Thus, we may have detected more birds in the morning because we were able to survey more points on a route during the peak singing period.

Our results suggest that surveying in the morning will maximize detection probability of wetland-dependent birds in the southeastern United States. We recommend that further studies be completed in other regions of North America to identify the optimal time of day to conduct surveys. Additional research is needed to examine the efficacy of night surveys for wetland-dependent birds that are rare or not present on SVI (e.g., Black Rail, Yellow Rail, and Virginia Rail).

ACKNOWLEDGMENTS

Monica Harris, Dale Shiver, and Charlotte Chumney provided logistical assistance on SVI. Robert Watt assisted with fieldwork. Wendy Gierhart provided GIS and logistical support. The manuscript benefited from comments provided by M. S. Woodrey and an anonymous reviewer.

LITERATURE CITED

Bookhout, T. A. 1995. Yellow Rail (*Coturnicops noveboracensis*). The birds of North America. Number 139.

Bystrak, D. 1981. The North American Breeding Bird Survey. Studies in Avian Biology 6:34–41.

Conway, C. J. 2007. Standardized North American Marsh Bird Monitoring Protocols. Wildlife Research Report Number 2007-04. USGS, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, USA.

Conway, C. J. and J. P. Gibbs. 2001. Factors influencing detection probabilities and the benefits of call-broadcast surveys for monitoring marsh birds. Final Report. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Conway, C. J. and C. P. Nadeau. 2006. Development and field testing of survey methods for a continental marsh bird monitoring program in North America. Wildlife Research Report Number 2005-11. USGS, Arizona Cooperative Fish and Wildlife Research Unit, Tucson, USA.

Conway, C. J., C. Sulzman, and B. A. Raulston. 2004. Factors affecting detection probability of California Black Rails. Journal of Wildlife Management 68:360–370.

Gibbs, J. P. and S. M. Melvin. 1993. Call-response surveys for monitoring breeding waterbirds. Journal of Wildlife Management 57:27–34.

Gibbs, J. P., S. M. Melvin, and F. A. Reid. 1992. American Bittern (*Botaurus lentiginosus*). The birds of North America. Number 18.

Grace, S. L. 2000. Final report of the vegetation survey and map report project, St. Vincent National Wildlife Refuge, Apalachicola, Florida. USGS-USFWS Research Partnership Program Project #1448-41650-97-N093. USGS, National Wetlands Research Center, Lafayette, Louisiana, USA.

Johnson, R. R. and J. J. Dinsmore. 1986. The use of tape-recorded calls to count Virginia Rails and Soras. Wilson Bulletin 98:303–306.

Lynch, J. 1995. Effects of point-count duration, time-of-day, and aural stimuli on detectability of migratory and resident bird species in Quintana Roo,

Mexico. Pages 1–6 *in* Monitoring bird populations by point counts (C. J. Ralph, J. R. Sauer, and S. Droege, Editors). USDA, Forest Service General Technical Report PSW-GTR-149. Pacific Southwest Research Station, Berkeley, California, USA.

Mangold, R. E. 1974. Research on shore and upland migratory birds in New Jersey: Clapper Rail studies, 1974 Report. Accelerated Research Program, Contract Number 14-16-0008-937. USDI, Fish and Wildlife Service, Trenton, New Jersey, USA.

Meanley, B. 1985. The marsh hen: a natural history of the Clapper Rail of the Atlantic coast salt marsh. Tidewater Publishing, Centreville, Maryland, USA.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408.

Reynard, G. B. 1974. Some vocalizations of the Black, Yellow and Virginia rails. Auk 91:747–756.

Robbins, C. S. 1981. Bird activity levels related to weather. Studies in Avian Biology 6:301–310.

Spear, L. B., S. B. Terrill, C. Lenihan, and P. Delevoryas. 1999. Effects of temporal and environmental factors on the probability of detecting California Black Rails. Journal of Field Ornithology 70:465–480.

Tacha, R. W. 1975. A survey of rail populations in Kansas with emphasis on Cheyenne Bottoms. Thesis. Fort Hays Kansas State College, Hays, USA.

Tango, P. J., G. D. Therres, D. F. Brinker, M. O'Brien, E. T. Blom, and H. L. Wierenga. 1997. Breeding distribution and relative abundance of marshbirds in Maryland: evaluation of a tape playback survey method. U.S. Fish and Wildlife Service Grant #14-48-009-95-1280 Final Report. USDI, Fish and Wildlife Service, Office of Migratory Bird Management, Denver, Colorado, USA.

The Wilson Journal of Ornithology 120(3):519–524, 2008

MALE SONG VARIATION OF GREEN VIOLETEAR (*COLIBRI THALASSINUS*) IN THE TALAMANCA MOUNTAIN RANGE, COSTA RICA

GILBERT BARRANTES,[1,4] CÉSAR SÁNCHEZ,[1] BRANKO HILJE,[2] AND RODOLFO JAFFÉ[3]

ABSTRACT.—We studied variation in acoustic and temporal characteristics of the static male song of the Green Violetear (*Colibri thalassinus*) in a single population in Costa Rica. The static song of 19 males was extremely variable. The song has two elements: the first was delivered exclusively at the beginning of each song while the second was present once, twice, or three times in the song of different males. Low frequency (LF), song duration (ΔT), and high frequency (HF) varied significantly among most individuals. The male population of Green Violetear has four song types that differ in acoustic and temporal characteristics. The great inter-male song variation suggests this type of vocalization may be under sexual selection. *Received 2 February 2007. Accepted 17 January 2008.*

Song variation among individual birds is well known for oscine and psittacid species (Farabaugh and Dooling 1996, Kroodsma 1996). Learning in these birds has an important role in syntaxes and structure of the song. This variation may have evolved to facilitate social interactions and/or by intra- or intersexual selection (Kroodsma 2004). Male reproductive success in birds is often associated with striking displays, such as complex songs, resulting from sexual selection (Catchpole 1982, Searcy and Yasukawa 1983, Johnsgard 1994, Kroodsma 2004).

Individual song variation is relatively unexplored in hummingbirds, another song-learning bird group (Baptista and Schuchmann 1990, Gaunt et al. 1994, Jarvis et al. 2000). Gaunt et al. (1994) showed that male Green Violetear (*Colibri thalassinus*) in neighboring populations share song types and similarity decreases with geographical distance. The extent of intra-population variation in male song has not previously been reported for this hummingbird.

Male Green Violetear show little (if any) aggressive physical interactions with other males during the breeding season (e.g., darting chases) and visual displays are apparently absent. Territorial males sing nearly continuously during courtship from before dawn until sunset (Slud 1964, Feinsinger 1977). Males begin to sing in September and some continue until the end of March, investing up to 84% of daily time to this activity (Skutch 1967, Wolf 1976). The objective of our study was to describe the variation in male song features within a population of Green Violetear.

METHODS

We conducted fieldwork at the Estación Biológica Cuericí, Talamanca Mountains, Costa Rica (09° 33′ N, 83° 40′ W; elevation 2,600 m) during the dry season in January 2004. The area is dominated by oak (*Quercus* spp.) forest intermixed with several successional growth stages with abundant flowering plants: *Fuchsia paniculata*, *Bomarea costaricensis*, *Lamourouxia lanceolata*, and *Centropogon* spp. We recorded the static songs (song uttered by perched birds) from 19 males singing from exposed perches, ranging from 8 to 25 m in height, on a 1.5-km transect along the primary road (4 m wide); 12 males were recorded one morning and seven the next morning. Singing males were separated by 20–100 m and perched at most 10 m into the forest ($n = 17$), facing the main road, or in a forest gap ($n = 2$). Each bird was recorded once for

[1] Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica.

[2] Instituto Tecnológico de Costa Rica, P. O. Box 159-7050, Cartago, Costa Rica.

[3] Apartado 68941, Altamira, Caracas 1062, Venezuela.

[4] Corresponding author; e-mail: gilbert.barrantes@gmail.com

at least 2 min or until the bird became silent. We recorded the hummingbirds sequentially as we walked along the road to avoid recording the same individual more than once. Because of their high density, we could, in most cases, listen to the hummingbird previously recorded when we began to record the next focal individual. We considered singing males as territorial individuals following Skutch (1967); however, identifying territory limits was difficult, due to few aggressive interactions by males of this species. We define a male territory as a circular area of 20 m in diameter around the perch the singing male was most frequently using.

We recorded songs using a Telinga Pro II Parabola and a Marantz PMD-222 tape recorder, and analyzed the songs using the program CANARY Version 1.2.1 (Charif et al. 1993). Tapes were deposited at the Laboratorio de Bioacústica, Escuela de Biología, Universidad de Costa Rica. Spectrograms were obtained with a filter bandwidth of 349.70 kHz, frame length of 256 points, and a sampling rate of 44,100 Hz. We identified the elements of the song, defining a song as a string of notes or elements, temporally separated from other such strings; an element was the shortest consistently recognizable trace on a sound spectrogram (Marler and Peters 1982). We randomly selected five songs separated by at least 10 sec to analyze the among-individual song variation from the total record of each hummingbird. We measured eight variables for each complete song: high frequency (HF), low frequency (LF), frequency range or bandwidth (ΔF) (HF-LF), peak frequency (PF, frequency with highest amplitude), peak time (PT, time with maximum amplitude), duration in seconds (ΔT), time elapsed between two consecutive songs (T1), and time between the first and the second element (T2). We also quantified the number of songs and elements delivered in a random selected minute for each individual.

We used a multiple analysis of variance (MANOVA) on six song variables (ΔT, LF, HF, PF, T1, and T2) to examine the difference of these variables among individuals (based on a Discriminant Function Analysis (DFA), ΔF and PT were excluded because they did not differ among individuals). One-way analyses of variance and *posteriori* tests (Duncan) were conducted to examine which particular variables differ among individuals. We classified the song of the hummingbirds into four types based on sonogram images, and used stepwise Discriminant Function Analysis (DFA) to test whether hummingbirds could be separated into four groups by their song features. We also recorded the following information during 6 days: non-systematic observations of aggressive interactions and presence of flower patches near perches of singing males. Means ± SD are presented.

RESULTS

The 19 male Green Violetears apparently held the same territories for at least 6 days as the same perches were occupied by singing males day after day and we assumed the same males were present. Territories included 2–3 perches from which males sang; they spent most of their time on one of them. The number of males singing appeared to decrease from the forest border to the interior, except when a gap was present, in which case the number of males singing increased near the gap edge.

Territories of the 19 recorded males varied by presence of flower patches used as nectar sources for hummingbirds. Twelve territories (main song perches) were within 10 m of large patches of *Fuchsia paniculata*, which were frequently visited by Green Violetears and Volcano Hummingbirds (*Selasphorus flammula*). Attacks between individual Green Violetears were rarely seen although the presence of an individual in a flower patch occasionally triggered an attack by a singing male. The absence of obvious sexual dimorphism prevented us from knowing whether these few attacks were directed preferentially at males.

Males sang from before dawn until dusk, only abandoning their perches to briefly visit nearby flower patches for feeding or to capture insects on the wing with short sallies. The song of all males included two different elements (Fig. 1). The first element (a) was produced only once in the song of all individuals. Element (b) occurred once in the song of nine males (song type 1), twice in the song of seven individuals (type 2), three times in two other males (type 3), and one or two times in songs produced by another male (type 4). On average, males produced 64.2 (± 8.8, range:

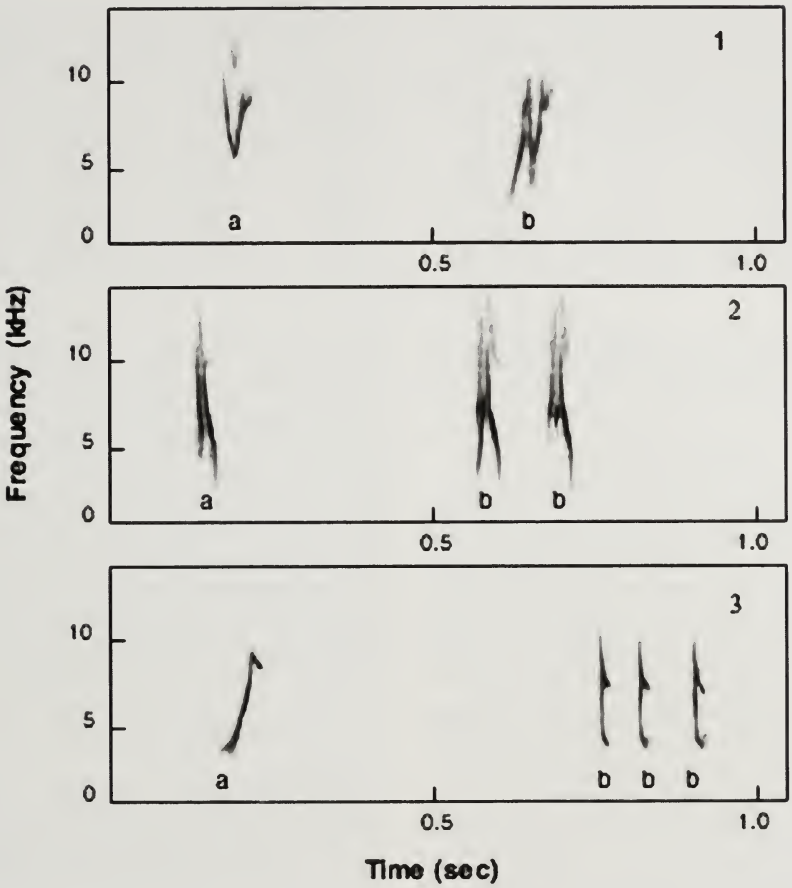


FIG. 1. Spectrograms of the variation in number of elements, and structural characteristics of elements and songs of three male *C. thalassinus*. Element (a) was present only once, at the beginning of each male's song, while presence of element (b) varied from one to three in songs of different males.

42–76.5) songs and 163.6 (± 33.7, range: 126–231) elements per minute.

Structurally, the frequency range and highest frequency were features of the static song that had the largest range (max-min values) for the 19 males: 11.06 and 9.08 kHz respectively (Table 1). The time between the first and the second element (T2), followed by frequency range (ΔF), had the largest variation (CV) among individuals. Number of songs delivered by individual per minute decreased with song duration ($r = -0.41$, $n = 19$, $P = 0.08$). However, the number of elements ($r = 0.17$, $n = 19$, $P = 0.49$) produced per minute was not related to ΔT. The large variation in ΔF was primarily caused by individual variation in both HF and LF.

We compared six characteristics of the complete song (ΔT, LF, HF, PF, T1, and T2) among individuals using a MANOVA. The comparison of all song features showed significant differences among individuals ($F_{108,414} = 21.66$, $P < 0.001$). Significant differences were also found among individuals when variables were analyzed separately (one-way ANOVA and Duncan tests). Variables that differed among most individuals were LF (16 males: $F_{18,76} = 57.64$, $P < 0.001$), ΔT (14 males: $F_{18,76} = 47.27$, $P < 0.001$), and HF (13 males: $F_{18,76} = 77.56$, $P < 0.001$). Variation among individuals was lower for PF (8 males: $F_{18,76} = 6.32$, $P < 0.001$), T1 (4 males: $F_{18,76} = 2.59$, $P = 0.002$), and T2 (4 males: $F_{18,76} = 26.62$, $P < 0.001$).

Male Green Violetears were divided in subgroups based on structural and temporal characteristics of their song. DFA separated the males of this population into four groups

TABLE 1. Characteristics of high frequency (HF), low frequency (LF), bandwidth (ΔF), peak frequency (PF), time duration (ΔT), time between two consecutive songs (T1), and time between the first and the second element (T2) for the complete song of 19 male Green Violetears in Costa Rica.

	HF (kHz)	LF (kHz)	ΔF (kHz)	PF (kHz)	ΔT (sec)	T1 (sec)	T2 (sec)
Mean	10.98	3.16	7.82	6.11	0.58	0.37	0.33
SD	2.19	0.57	2.36	0.81	0.10	0.03	0.15
CV	19.90	17.98	30.17	13.31	17.73	8.86	44.41
Range	9.04–18.12	2.08–4.82	4.28–15.34	4.05–8.53	0.42–0.95	0.30–0.51	0.069–0.84

($F_{15,240} = 11.98$, $P < 0.0001$) based on six variables (ΔT, LF, HF, PF, T1, and T2), and classified 82% of the songs correctly.

DISCUSSION

The difference in characteristics of the static song among male Green Violetears was high. This difference individualizes most singing males in the population, suggesting a possible role of inter- and intra-sexual selection (Morton 1986, Searcy and Andersson 1986); however, other factors such as age may also affect song characteristics. Frequency range in the song of *C. thalassinus* is possibly the feature from which the receiver (e.g., a female) obtains greater information, particularly when the song is composed by short, broad bandwidth elements or notes (Fig. 1, Table 1). This characteristic permits more precise location of singing males (Smith et al. 1978, Richards and Wiley 1980). Additionally, males producing songs with a wide frequency range may conceal the songs of other males, if these males' songs have a narrower bandwidth that fit in part of the range of frequencies of other males.

Despite the high variation in this population of male Green Violetears, groups of males produced similar song types. This suggests the presence of "different dialects" in a single population. However, causes of inter-group song differentiation are difficult to explain. Dialects usually evolve through geographic or microgeographic isolation (Kroodsma 1996) but, in this case, geographic isolation seems not to be the cause, since this species breeds in the area and then migrates to lower elevation during the non-breeding season (Skutch 1967). In addition, young hear songs of adult males as males sing well beyond when fledglings abandon their nests (GB, pers. obs.). A possible explanation is the "song relearn hypothesis" proposed by Kroodsma (2004) to explain temporal song variation in dialects of the Three-wattled Bellbird (*Procnias tricarunculatus*). This hypothesis proposes that adult birds "relearn" their songs throughout their life, and modify their songs through competition (by imitation) with familiar rivals. For this hypothesis to be possible, groups of males have to hear and recognize neighboring males (Aoki 1989); this is the case with Green Violetear. Consequently, at a particular time lag, different songs could be present in a single population. However, spatial distribution of song types is needed to begin testing this hypothesis.

The information available allows us to compare variation of song traits of *C. thalassinus* with other Trochilinae hummingbirds. The number of elements in the song of *C. thalassinus* is small compared to songs of Anna's Hummingbird (*Calypte anna*) (Stiles 1982), Blue-throated Hummingbird (*Lampornis clemenciae*) (Ficken et al. 2000), Amethyst-throated Hummingbird (*L. amethystinus*), and Green-throated Mountaingem (*L. viridipallens*). The number of elements is similar to Magnificent Hummingbird (*Eugenes fulgens*) (Ornelas et al. 2002) and more complex (e.g., more elements and frequency modulation) than the static song of its congener Sparkling Violetear (*Colibri coruscans*) (Gaunt et al. 1994). A characteristic present in all songs of this small sample of hummingbirds is the wide frequency range (bandwidth), although both species of the genus *Colibri* present the narrowest bandwidth. Song complexity is not higher in those species lacking visual displays, such as *C. thalassinus*, when compared to species with complex visual displays, such as *C. anna* and *L. amethystinus*. These results should be viewed with caution because number of elements and acoustic structure of hum-

mingbird songs may be strongly influenced by environmental and phylogenetic features (Irwin 1988, McCracken and Sheldon 1997). These aspects can be more closely analyzed within the monophyletic genus *Colibri*. When features of the song are compared between *C. thalassinus* and *C. coruscans*, the two highland species of the genus (Gaunt et al. 1994), the static song of *C. thalassinus* has a higher number of elements. However, *C. coruscans* produces a "dynamic song" that males sing during a diving flight as part of the courtship display, which is absent in *C. thalassinus*. This supports Wagner's (1954) suggestion that species lacking elaborate dynamic songs have complex static songs, and suggests the two highland species of the genus have evolved different courtship strategies. The other two species in the genus, *C. delphinae* and *C. serrirostris* are mid-elevation and apparently territorial (Stiles and Skutch 1989, Schuchmann 1999). Little is known about the vocalizations of these two species.

ACKNOWLEDGMENTS

We thank J. R. Eberhard, D. E. Kroodsma, C. E. Braun, and two anonymous reviewers for helpful and critical comments on the manuscript, and Luis Sandoval for helping with the statistical analysis. We also thank the Universidad de Costa Rica for financial support and The Organization for Tropical Studies and Estación Biológica Cuericí for logistical support.

LITERATURE CITED

Aoki, K. 1989. A sexual-selection model for the evolution of imitative learning of song in polygynous birds. American Naturalist 134:599–612.

Baptista, L. F. and K. L. Schuchmann. 1990. Song learning in the Anna Hummingbird (*Calypte anna*). Ethology 84:15–26.

Catchpole, C. K. 1982. The evolution of bird sounds in relation to mating and spacing behaviour. Pages 297–319 *in* Acoustic communication in birds. Production, perception, and design features of sounds (D. E. Kroodsma and E. H. Miller, Editors). Academic Press, New York, USA.

Charif, R. A., S. Mitchell, and C. W. Clark. 1993. Canary 1.1 user's manual. Cornell Laboratory of Ornithology, Ithaca, New York, USA.

Farabaugh, S. M. and R. J. Dooling. 1996. Acoustic communication in parrots: laboratory and field experiments of Budgerigars, *Melopsittacus unulatus*. Pages 97–117 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Editors). Cornell University Press, New York, USA.

Feinsinger, P. 1977. Notes on the hummingbirds of Monterverde, Cordillera de Tilarán, Costa Rica. Wilson Bulletin 89:159–164.

Ficken, M. S., K. M. Rush, S. J. Taylor, and D. R. Powers. 2000. Blue-throated Hummingbird song: pinnacle on nonoscine vocalizations. Auk 117: 120–128.

Gaunt, S. L. L., L. F. Baptista, J. E. Sánchez, and D. Hernández. 1994. Song learning as evidenced from song sharing in two hummingbird species (*Colibri coruscans* and *C. thalassinus*). Auk 111: 87–103.

Irwin, R. E. 1988. The evolutionary importance of behavioral development: the ontogeny and phylogeny of bird song. Animal Behaviour 36:814–824.

Jarvis, E. D., S. Ribeiro, M. L. da Silva, D. Ventura, J. Vielliard, and C. V. Mello. 2000. Behaviourally driven gene expression reveals song nuclei in hummingbird brain. Nature 406:628–632.

Johnsgard, P. A. 1994. Arena birds: sexual selection and behavior. Smithsonian Institution Press, Washington, D.C., USA.

Kroodsma, D. 1996. Ecology of passerine song development. Pages 3–19 *in* Ecology and evolution of acoustic communication in birds (D. E. Kroodsma and E. H. Miller, Editors). Cornell University Press, Ithaca, New York, USA.

Kroodsma, D. 2004. The diversity and plasticity of birdsong. Pages 108–131 *in* Nature's music. The science of birdsong (P. Marler and H. Slabbekoorn, Editors). Academic Press, New York, USA.

Marler, P. and S. Peters. 1982. Subsong and plastic song: their role in the vocal learning process. Pages 25–50 *in* Acoustic communication in birds. Production, perception, and design features of sounds (D. E. Kroodsma and E. H. Miller, Editors). Academic Press, New York, USA.

McCracken, K. G. and F. H. Sheldon. 1997. Avian vocalizations and phylogenetic signal. Proceedings of the National Academy of Science USA 94: 3833–3836.

Morton, E. S. 1986. Prediction from the ranging hypothesis for the evolution of long distance signals in birds. Behaviour 99:65–86.

Ornelas, J. F., C. Gonzáles, and J. Uribe. 2002. Complex vocalizations and aerial displays of the Amethyst-throated Hummingbird (*Lampornis amethystinus*). Auk 119:1141–1149.

Richards, D. G. and R. H. Wiley. 1980. Reverberation and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. American Naturalist 115:381–399.

Schuchmann, K. L. 1999. Family Trochilidae (hummingbirds). Pages 468–680 *in* Handbook of birds of the world. Volume 5. Barn Owls to hummingbirds (J. Del Hoyo, A. Elliott, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

Searcy, W. A. and M. Andersson. 1986. Sexual selection and the evolution of song. Annual Review of Ecology and Systematics 17:507–533.

Searcy, W. A. and K. Yasukawa. 1983. Sexual se-

lection and Red-winged Blackbirds. American Scientist 71:166–174.

SKUTCH, A. F. 1967. Life histories of Central American highland birds. Nuttall Ornithological Club Number 7. Cambridge, Massachusetts, USA.

SLUD, P. 1964. The birds of Costa Rica. Distribution and ecology. Bulletin of the American Museum of Natural History 128:1–430.

SMITH, W. J., J. PAWLUKIEWICZ, AND S. T. SMITH. 1978. Kinds of activities correlated with singing patterns of the Yellow-throated Vireo. Animal Behaviour 26:862–884.

STILES, F. G. 1982. Aggressive and courtship displays of the male Anna's Hummingbird. Condor 84: 208–225.

STILES, F. G. AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

WAGNER, H. O. 1954. Versuche einer analyse der kolibribalz. Zeitschrift für Tierpsychologie 11:182–212.

WOLF, L. L. 1976. Avifauna of the Cerro de la Muerte region Costa Rica. American Museum Novitates 2606:1–37.

The Wilson Journal of Ornithology 120(3):525–530, 2008

METABOLIZABLE ENERGY IN CHINESE TALLOW FRUIT FOR YELLOW-RUMPED WARBLERS, NORTHERN CARDINALS, AND AMERICAN ROBINS

MICHAEL J. BALDWIN,[1,3] WYLIE C. BARROW JR.,[1] CLINTON JESKE,[1] AND FRANK C. ROHWER[2]

ABSTRACT.—The invasive exotic Chinese tallow tree (*Triadica sebifera*) produces an abundant fruit crop, which is primarily bird-dispersed. The fruit pulp of tallow is lipid-rich, high in saturated fatty acids, and consumed by many bird species. Long-chained fatty acids can be difficult for many birds to digest and we investigated the ability of tallow consumers to assimilate energy in the pulp. We used the total collection method and compared apparent metabolizable energy (AME) of tallow fruit for three species of birds with differing fruit composition in their natural diets. All birds exhibited nitrogen deficits and lost body mass during the trials. Northern Cardinals (*Cardinalis cardinalis*) lost more mass (8.73%/day) than Yellow-rumped Warblers (*Dendroica coronata*) (5.29%/day) and American Robins (*Turdus migratorius*) (5.48%/day), and had larger nitrogen deficits (−120.1 mg N/g diet) than both species as well (−36.4 mg N/g diet and −68.9 mg N/g diet, respectively). Food intake relative to metabolic body mass was highest in Yellow-rumped Warblers (0.70 g-dry/$g^{0.75}$·day). Northern Cardinal and American Robin food intake was lower and did not differ from each other (both species: 0.13 g-dry/$g^{0.75}$·day). Nitrogen corrected values of AME were used to make species comparisons. Yellow-rumped-Warblers exhibited the highest values of AME (30.00 kJ/g), followed by American Robins (23.90 kJ/g), and Northern Cardinals (14.34 kJ/g). We suggest tallow may be an important winter food source for Yellow-rumped Warblers where their ranges overlap. *Received 5 July 2006. Accepted 14 October 2007.*

The Chinese tallow tree (*Triadica sebifera*) is an invasive, non-native tree from Southeast Asia. It is now common in many areas along the northern Gulf of Mexico and south Atlantic coast (Scheld and Cowles 1981, Harcombe et al. 1993, Renne et al. 2000) and often exists in near monospecific stands (Baldwin 2005). It is primarily a bird-dispersed plant producing an abundant fruit crop in the fall that can persist until early spring. The fruit contains a hard seed surrounded by waxy pulp, which is largely comprised of saturated fatty acids (42.5–75.1% of total fatty acids) (Khan et al. 1973, Raie et al. 1983, Xu et al. 1991). Many animals exhibit poor assimilation of high-melting point fatty acids (Scott et al. 1976) and their digestion may require specialized physiological traits (Place and Stiles 1992). Consequently, tallow may provide poor quality food to most birds despite its high energetic value (33.5 kJ/g, range of other common plant species = 14.91–30.23 kJ/g; W. C. Barrow Jr. and C. Jeske, unpubl. data) and consumption by many species (24 species: Conway et al. 2002; 64 species: W. C. Barrow Jr. and W. R. Fontenot, unpubl. data). This issue has become more significant with the increasing expansion of tallow in the region.

We conducted feeding trials on three species of birds with varying diets all known to consume tallow fruit. Yellow-rumped Warblers (*Dendroica coronata*) were selected because they were the most frequent tallow consumer in coastal Texas (Conway et al. 2002) and have a specialized digestive system that allows them to assimilate waxy foods such as wax myrtle (*Morella cerifera*) and northern bayberry (*M. pensylvanica*) fruit (Place and Stiles 1992). They were also the most abundant bird observed in tallow-dominated woodlands during winter in southwest Louisiana (Baldwin 2005). Yellow-rumped Warblers can assimilate high-melting point fatty acids, but they prefer unsaturated to saturated fatty acids (McWilliams et al. 2002). American Robins (*Turdus migratorius*) and Northern Cardinals (*Cardinalis cardinalis*) were selected based on their relatively high consumption of tallow fruit (Renne et al. 2000, 2002). These two species were the second and third most abundant birds detected in tallow woodlands during

[1] U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Boulevard, Lafayette, LA 70506, USA.

[2] School of Renewable Natural Resources, Louisiana State University, Baton Rouge, LA 70803, USA.

[3] Corresponding author;
e-mail: michael_baldwin@usgs.gov

winter (Baldwin 2005). Neither species is known to have specialized digestive traits similar to the Yellow-rumped Warbler. American Robins have exhibited relatively high digestive efficiencies of lipids (Witmer and Van Soest 1998, Lepczyk et al. 2000) and Zurovchak et al. (1999) found no change in absorption efficiency with increasing lipid levels in a test diet. These studies did not test for differences in fatty acid composition and the diets examined were comprised primarily of unsaturated fatty acids. Zurovchak (1997) measured food preferences of American Robins offered synthetic fruits high in either saturated or unsaturated fatty acids and observed preferences for the latter by most individuals tested; none preferred saturated fatty acids. Zurovchak (1997) suggested the few individuals that exhibited no preference were likely selecting fruit based on color. Willson and Harmeson (1973) studied Northern Cardinal seed preferences and found no correlation between seed preference and lipid concentration. No information is available on Cardinal fruit preferences based on lipid content or fatty acid composition, but they are known to consume high-lipid fruit (Fontenot 1998, Borgmann et al. 2004).

Our objective was to examine how well Yellow-rumped Warblers, Northern Cardinals, and American Robins could metabolize the available energy in tallow fruit during controlled feeding trials. We hypothesized that Yellow-rumped Warblers would assimilate a greater amount of the available energy than Northern Cardinals and American Robins because of their diet and specialized digestive traits.

METHODS

Capture and Care of Birds.—Yellow-rumped Warblers ($n = 9$), Northern Cardinals ($n = 10$), and American Robins ($n = 5$) were captured near Lafayette, Louisiana in the winters of 2001–2002 and 2002–2003, and transported to an indoor environmental chamber where they were kept under controlled temperatures (20° C) and photoperiod (10.5L: 13.5D). Birds were housed individually in 30 × 36 × 36 cm metal cages. Water and maintenance diet were provided *ad libitum.* The diet consisted of a commercial mash designed for captive birds (Avian-Fare and/or Soft-billed-Fare) mixed in a plastic food cup with tallow fruit and mealworms. In addition, Yellow-rumped Warblers were supplemented with fruit from wax myrtle and poison ivy (*Toxicodendron radicans*) while American Robins and Northern Cardinals were given fruit from hackberry (*Celtis laevigata*) and deciduous holly (*Ilex decidua*). Northern Cardinals were also provided sunflower (*Helianthus* spp.) and safflower (*Carthamus tinctorius*) seeds.

The total collection method (Servello et al. 2005) was used to measure apparent metabolizable energy (AME) in tallow fruit. Birds were allowed a minimum of 12–14 days to acclimate to captivity prior to onset of AME trials and no individual was used more than once. Birds were only offered tallow fruit during feeding trials. Whole fruits (seed included) were fed to Northern Cardinals and American Robins, while Yellow-rumped Warblers were presented with pulp only. Yellow-rumped Warblers feed on tallow by pecking or scraping off the waxy, outer layer. Pulp was removed from tallow fruit using a dissecting needle or by rubbing fruit over a 2-mm sieve. Northern Cardinals and American Robins did not digest the seed, and all AME estimates were calculated for pulp only.

Fruit was placed into a plastic food cup and weighed prior to each feeding. The first day of the AME trial was used to remove nonexperimental foods from the digestive tract and no fecal material was collected. Fecal material was collected daily after day one; the remaining food was removed and weighed, including spilled food, and fresh food was weighed and provided to the birds. Food and fecal samples were placed in scintillation vials, vacuum-dried, and stored at −80° C. Gross energy in food and fecal samples was measured with a Parr 1261 Isoperibol Bomb Calorimeter.

Values for AME may be influenced by nitrogen loss/gain flux during feeding trials caused by protein tissue growth/catabolism (Scott et al. 1976), particularly for low-protein foods such as fruit. This affects endogenous urinary nitrogen levels in an individual's feces and zero nitrogen balance AME calculations were needed. Percent total nitrogen in food and fecal samples was measured with a Thermo Finnigan® FlashEA 1112 Elemental Analyzer. Previous studies have used the Kjeldahl

method to measure nitrogen composition (Scott et al. 1976, Carl and Brown 1985, Servello et al. 2005). Our method was chosen because it is as accurate as the Kjeldahl method, allows for smaller sample size, and requires less preparation and run time (Matejovic 1995). Amount of nitrogen lost/retained was measured as the difference in nitrogen consumed via tallow pulp and the amount of nitrogen in the feces. Nitrogen corrected AME values were calculated by: (AME (kJ/g) = $4.1841 \cdot \{(F \cdot FE) - [(X \cdot XE + 8.22 \cdot (NF - NE)]\}/F$), where F and X equal the dry weights (g) of ingested food and excrement, FE and XE equal the energy (kcal/g) of ingested food and excrement, 8.22 is the energy constant (kcal/g) of nitrogen in uric acid, and NF and NE equal the grams of nitrogen in the diet and excrement, respectively (Scott et al. 1976).

Statistical Analyses.—Dry food intake relative to metabolic body mass ($g/g^{0.75} \cdot day$), body mass change, and nitrogen corrected AME values (kJ/g) for tallow pulp were compared using nonparametric Kruskal-Wallis tests (Conover 1980) in SAS (Proc NPAR1WAY, SAS Institute Inc. 1999). Species differences in nitrogen flux (mg N/g) were compared with ANOVA. Contrasts were performed on ranks with Tukey's pairwise comparisons (Proc MIXED, SAS Institute Inc. 1999) when the null hypothesis of no difference among species was rejected ($\alpha = 0.05$). One Northern Cardinal exhibited a negative AME; it was treated as an outlier and excluded in the analysis.

RESULTS

Mean (± SD) gross energy and percent total nitrogen in tallow pulp were 34.43 ± 0.12 kJ/g and 0.32 ± 0.004%, respectively. Food intake ($g/g^{0.75} \cdot day$) varied among species ($\chi^2 = 11.14$, $P = 0.004$) and was highest in Yellow-rumped Warblers, but did not differ between Northern Cardinals and American Robins (Table 1). All individuals lost body mass during the trials and exhibited nitrogen deficits. Mass loss differed among species ($\chi^2 = 11.71$, $P = 0.003$) and was highest in Northern Cardinals (Table 1). The amount of nitrogen lost per gram of tallow consumed was not equal between species ($F_{2,20} = 29.4$, $P < 0.001$), and was highest in Northern Cardinals

TABLE 1. Food intake relative to metabolic body mass, body mass loss, nitrogen balance, uncorrected AME, and nitrogen corrected AME by three bird species. ANOVA was used to make species comparisons in nitrogen balance. Food intake, body mass loss, and nitrogen-corrected AME were compared with Kruskal-Wallis tests. Pairwise comparisons were made on the ranks using Tukey's *post-hoc* test ($\alpha = 0.05$). Values with the same letter in parentheses are not significantly different. Means ± SE.

Bird species	*n*	Food intake ($g - dry/g^{0.75} \cdot day$)	Body mass loss (%/day)	Nitrogen balance (mg N lost/g diet)	Uncorrected AME (kJ/g)	Nitrogen corrected AME (kJ/g)
Yellow-rumped Warbler	9	0.70 ± 0.12 (A)	5.29 ± 0.71 (A)	−36.4 ± 2.3 (A)	29.79 ± 0.81	30.00 ± 0.73 (A)
Northern Cardinal	9	0.13 ± 0.02 (B)	8.73 ± 0.38 (B)	−120.1 ± 10.4 (B)	10.15 ± 2.95	14.34 ± 2.54 (B)
American Robin	5	0.13 ± 0.03 (B)	5.48 ± 0.37 (A)	−68.9 ± 11.5 (A)	23.66 ± 0.65	23.90 ± 0.76 (C)

and lowest in Yellow-rumped Warblers (Table 1). Pair-wise comparisons between uncorrected and nitrogen corrected AME results for all birds pooled were different (*t*-test: $t = -3.61$, $P = 0.002$); therefore, we used nitrogen corrected AME values ($\bar{x} \pm$ SE) for species comparisons. AME differed among bird species ($\chi^2 = 16.02$, $P < 0.001$) and was highest for Yellow-rumped Warblers (30.00 ± 0.73 kJ/g) followed by American Robins (23.90 ± 0.76 kJ/g) and Northern Cardinals (14.34 ± 2.54 kJ/g).

DISCUSSION

Assimilation of AME of tallow differed significantly among species and was highest in Yellow-rumped Warblers. These results support our hypothesis that Yellow-rumped Warblers would exhibit higher values of AME due to their specialized digestive traits as described by Place and Stiles (1992). Northern Cardinals exhibited high variability among individuals for values of AME. We considered gender as a source of this variation, but found no evidence of it being a factor. Others have similarly observed high variability in the digestive efficiencies of Northern Cardinals fed different seeds (Willson and Harmeson 1973, Shuman et al. 1989). Willson and Harmeson (1973) were unable to attribute their results to individual variation in feces mass, feces caloric content, or mass of ingested food. We similarly were unable to relate these factors, nor the extent of body mass loss, to individual variability in AME. We do entertain the possibility that certain individuals did not acclimate well to tallow during the pre-trial period. This could occur if some Northern Cardinals avoided tallow fruit in the maintenance diet due to dietary preferences or an aversion to a novel food source (Greenberg 1990). We did not observe high variability in AME values among individual American Robins or Yellow-rumped Warblers in this study.

Northern Cardinals are considered important dispersers of tallow in Louisiana (Renne et al. 2002), but our results suggest that tallow is not a valuable energy source for them. Their ability to metabolize tallow was less than half that observed for Yellow-rumped Warblers. The relatively high AME values observed for American Robins implies that tallow could serve as an alternative fall and winter food source. None of the species examined could subsist solely on tallow fruit for any length of time, although this is not entirely unexpected for birds on fruit diets (Izhaki and Safriel 1989, Levey and Karasov 1989, Mack 1990, Wheelwright 1991). Fruits generally contain low amounts of protein (Snow 1971, Morton 1973), but the percent total nitrogen (used to estimate crude protein) in tallow pulp was low (the lowest of 36 species of fruit pulp tested, W. C. Barrow Jr. and C. Jeske, unpubl. data; and nearly a third less than the minimum required by American Robins, Witmer 1998) and all individuals expressed nitrogen deficits.

The potential impact of tallow's introduction on Yellow-rumped Warblers is of particular interest. This species exhibits a facultative migration that is dependent on food abundance and climatic conditions (Terrill and Ohmart 1984). Their abundance has been positively correlated to wax myrtle fruit abundance in South Carolina (Kwit et al. 2004) and Florida (Borgmann et al. 2004). Like tallow, wax myrtle produces abundant fruit that is high in saturated fatty acids (Place and Stiles 1992). We hypothesize that tallow may influence the local winter distribution of Yellow-rumped Warblers in the southeastern United States due to their migratory behavior and the similarities between tallow and wax myrtle fruit. Anecdotal evidence is in support of this hypothesis. Evidence of non-native plants affecting species distributions has been presented before. Stiles (1982) hypothesized the northward expansion of the Northern Mockingbird's (*Mimus polyglottos*) winter range in the northeastern United States was linked to the spread of multiflora rose (*Rosa multiflora*). Multiflora rose has also been linked to the regional increase of Veeries (*Catharus fuscescens*) in the mid-Atlantic Piedmont forest due to an increase in available nesting sites (Heckscher 2004). More research is needed to understand the full effects of tallow on the diet and distribution of birds.

ACKNOWLEDGMENTS

This study was funded by the U.S. Geological Survey, National Wetlands Research Center. We thank C. D. Pearson, K. M. Mack, P. R. Fontenot, and Jerrl Thompson for field and laboratory support. Editorial comments and advice were provided by P. C. Stouffer, H. Q. Baldwin, J. A. Davis, D. J. Johnson, C. E. Braun, and two anonymous reviewers. Any use of trade, prod-

uct, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. All research with captive birds was under permit (2001-8717-037) and approval by the Institutional Animal Care and Use Committee (IACUC).

LITERATURE CITED

Baldwin, M. J. 2005. Winter bird use of the Chinese tallow tree in Louisiana. Thesis. Louisiana State University, Baton Rouge, USA.

Borgmann, K. L., S. F. Pearson, D. J. Levey, and C. H. Greenberg. 2004. Wintering Yellow-rumped Warblers (*Dendroica coronata*) track manipulated abundance of *Myrica cerifera* fruits. Auk 121:74–87.

Carl, G. R. and R. D. Brown. 1985. Protein requirement of adult collared peccaries. Journal of Wildlife Management 49:351–355.

Conover, W. J. 1980. Practical nonparametric statistics. Second Edition. John Wiley and Sons, New York, USA.

Conway, W. C., L. M. Smith, and J. F. Bergan. 2002. Avian use of Chinese tallow seeds in coastal Texas. Southwestern Naturalist 47:550–556.

Fontenot, W. R. 1998. A survey of bird frugivory in Louisiana. Journal of Louisiana Ornithology 4: 31–58.

Greenberg, R. 1990. Ecological plasticity, neophobia, and resource use in birds. Studies in Avian Biology 13:431–437.

Harcombe, P. A., G. N. Cameron, and E. G. Glumac. 1993. Above-ground net primary productivity in adjacent grassland and woodland on the coastal prairie of Texas, USA. Journal of Vegetation Science 4:521–530.

Heckscher, C. M. 2004. Veery nest sites in a Mid-Atlantic Piedmont forest: vegetative physiognomy and use of alien shrubs. American Midland Naturalist 151:326–337.

Izhaki, I. and U. N. Safriel. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. Oikos 54:23–32.

Khan, F. W., K. Khan, and M. N. Malik. 1973. Vegetable tallow and stillingia oil from the fruits of *Sapium sebiferum* Roxb. Pakistan Journal of Forestry 23:257–266.

Kwit, C., D. J. Levey, C. H. Greenberg, S. F. Pearson, J. P. McCarty, S. Sargent, and R. L. Mumme. 2004. Fruit abundance and local distribution of wintering Hermit Thrushes (*Catharus guttatus*) and Yellow-rumped Warblers (*Dendroica coronata*) in South Carolina. Auk 121:46–57.

Lepczyk, C. A., K. G. Murray, K. Winnett-Murray, P. Bartell, E. Geyer, and T. Work. 2000. Seasonal fruit preferences for lipids and sugars by American Robins. Auk 117:709–717.

Levey, D. J. and W. H. Karasov. 1989. Digestive responses of temperate birds switched to fruit or insect diets. Auk 106:675–686.

Mack, A. L. 1990. Is frugivory limited by secondary compounds in fruits? Oikos 57:135–138.

Matejovic, I. 1995. Total nitrogen in plant material determination by means of dry combustion: a possible alternative to determination by Kjeldahl digestion. Communications in Soil Science and Plant Analysis 26:2217–2229.

McWilliams, S. R., S. B. Kearney, and W. H. Karasov. 2002. Diet preferences of warblers for specific fatty acids in relation to nutritional requirements and digestive capabilities. Journal of Avian Biology 33:167–174.

Morton, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. American Naturalist 107:8–22.

Place, A. and E. W. Stiles. 1992. Living off the wax of the land: bayberries and Yellow-rumped Warblers. Auk 109:334–345.

Raie, M. Y., S. Zaka, S. Iqbal, A. W. Sabir, and S. A. Khan. 1983. *Sapium sebiferum* oil and fat analysis by chromatography. Fette Seifen Anstrichmittel 85:359–362.

Renne, I. J., S. A. Gauthreaux Jr., and C. A. Gresham. 2000. Seed dispersal of the Chinese tallow tree (*Sapium sebiferum* [L.] Roxb.) by birds in coastal South Carolina. American Midland Naturalist 144:202–215.

Renne, I. J., W. C. Barrow Jr., L. A. Johnson Randall, and W. C. Bridges Jr. 2002. Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness in South Carolina and Louisiana, USA. Diversity and Distributions 8:285–295.

SAS Institute Inc. 1999. SAS OnlineDoc®. Version 8. SAS Institute Inc., Cary, North Carolina, USA.

Scheld, H. W. and J. R. Cowles. 1981. Woody biomass potential of the Chinese tallow tree. Economic Botany 35:391–397.

Scott, M. L., M. C. Nesheim, and R. J. Young. 1976. Nutrition of the chicken. M. L. Scott and Associates, Ithaca, New York, USA.

Servello, F. A., E. C. Hellgren, and S. R. McWilliams. 2005. Techniques for wildlife nutritional ecology. Pages 554–590 *in* Techniques for wildlife investigations and management (C. E. Braun, Editor). Sixth Edition. The Wildlife Society, Bethesda, Maryland, USA.

Shuman, T. W., R. J. Robel, J. L. Zimmerman, and K. E. Kemp. 1989. Variance in digestive efficiencies of four sympatric avian granivores. Auk 106:324–326.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113:194–202.

Stiles, E. W. 1982. Expansions of Mockingbird and multiflora rose in the northeastern United States and Canada. American Birds 36:358–364.

Terrill, S. B. and R. D. Ohmart. 1984. Facultative extension of fall migration by Yellow-rumped Warblers (*Dendroica coronata*). Auk 101:427–438.

Wheelwright, N. T. 1991. How long do fruit-eating birds stay in the plants where they feed? Biotropica 23:29–40.

Willson, M. F. and J. C. Harmeson. 1973. Seed preferences and digestive efficiency of Cardinals and Song Sparrows. Condor 75:225–234.

Witmer, M. C. 1998. Ecological and evolutionary implications of energy and protein requirements of avian frugivores eating sugary diets. Physiological Zoology 71:599–610.

Witmer, M. C. and P. J. Van Soest. 1998. Contrasting digestive strategies of fruit-eating birds. Functional Ecology 12:728–741.

Xu, J., T. Chikashige, S. Meguro, and S. Kawachi. 1991. Effective utilization of Stillingia or Chinese tallow-tree (*Sapium sebiferum*) fruits. Mokuzai Gakkaishi 37:494–498.

Zurovchak, J. G. 1997. Nutritional role of high-lipid fruits in the diet of migrant thrushes. Dissertation. Rutgers University, New Brunswick, New Jersey, USA.

Zurovchak, J. G., E. W. Stiles, and A. R. Place. 1999. Effect of dietary lipid level on lipid passage rate and lipid absorption efficiency in American Robins (*Turdus migratorius*). Journal of Experimental Zoology 283:408–417.

The Wilson Journal of Ornithology 120(3):531–544, 2008

FORAGING ECOLOGY OF HIGH ANDEAN INSECTIVOROUS BIRDS IN REMNANT *POLYLEPIS* FOREST PATCHES

HUW LLOYD[1]

ABSTRACT.—I examined how High Andean insectivorous birds partition resources in remnant *Polylepis* forest patches at three locations in the Cordillera Vilcanota, southern Peru. A number of distinctive guilds were identified within the bird community based on the manner and location of foraging displayed by each species. Important dimensions that enabled differentiation amongst guild co-members were those that supported the partitioning of resources between guilds. The significant disproportionate use of substrates and prey-attack maneuvers by birds indicated substrate specialization within the insectivorous *Polylepis* bird community. These specializations provide a means by which *Polylepis* insectivores fit syntopically along a resource gradient. Insectivores demonstrated a differential response to foraging in smaller patches, and changes in the foraging regimes of four guilds between large and small patches were frequent. The most abundant insectivores in small patches were the least diverse foragers; they compensated behaviorally for changes in patch habitat quality by using fewer substrates and prey-attack maneuvers. Guild members that shifted their foraging regime to use fewer attack maneuvers were also more tolerant of small patches. Small *Polylepis* patches have a significant role in fragmented High-Andean ecosystem functioning by providing essential foraging habitat for insectivorous birds.
Received 16 April 2007. Accepted 18 November 2007.

Small patches or scattered trees are a common feature of many fragmented landscapes (e.g., Guevara and Laborde 1993, Fischer and Lindenmayer 2002, Manning et al. 2006) and are central to many conservation strategies (e.g., Diamond et al. 1987, Fischer et al. 2005, Manning et al. 2006). Forest patches differ in size and vegetation composition, factors that are likely to influence the variety and quantity of food resources (Muhlenburg et al. 1977, Fæth and Kane 1978, Jaenike 1978). Few studies have examined the foraging ecology of bird species in different forest patch size categories to identify which species are more affected by habitat changes than others, and the extent to which birds are capable of behaviorally compensating for habitat changes (e.g., Maurer and Whitmore 1981). Examining the trophic-structure of remnant patch specialists and, in particular, how different foraging guilds vary in response to foraging in patches of different sizes, may provide a more complete understanding of the factors that govern overall bird community structure in fragmented landscapes. Furthermore, these analyses could identify how small patches could serve as focal tools for habitat management.

[1] Department of Environmental and Geographical Sciences, Manchester Metropolitan University, Chester Street, Manchester, United Kingdom. M1 5GD; e-mail: h.lloyd@mmu.ac.uk

Polylepis woodland is a distinctive, high-elevation Andean forest habitat that occurs above cloud level (3,500–5,000 m) as patches of woody vegetation surrounded by paramo (e.g., *Festuca* species) or puna (e.g., *Ichu* species) grass and shrub (e.g., *Baccharis* species) communities (Stotz et al. 1996). These high-altitude woodlands are relicts of a once-widespread habitat (Ellenberg 1958, Kessler 2002) and comprise mainly evergreen trees of the genus *Polylepis* (Rosaceae) which are highly drought tolerant (Fjeldså 1993, Stotz et al. 1996). The trunk and branches are laminated with brown-reddish bark that peels off in paper-like sheets as a protection against extremely low temperatures, and often have mosses and lichens growing on them (Capriles and Flores 2002).

Previous studies have shown that a number of specialized bird species are associated with *Polylepis* forests and show high habitat-restricted endemism (Fjeldså 1992, 1993) and forest patch specialization (Lloyd and Marsden in press). Little is known about the foraging ecology of *Polylepis* bird species (Herzog et al. 2002), the majority of which are described as insectivorous (Herzog et al. 2003). This information is important because *Polylepis* woodlands are impacted by humans in several ways (Renison et al. 2006) including firewood collection (Fjeldså 1993), fire management (Renison et al. 2002), browsing

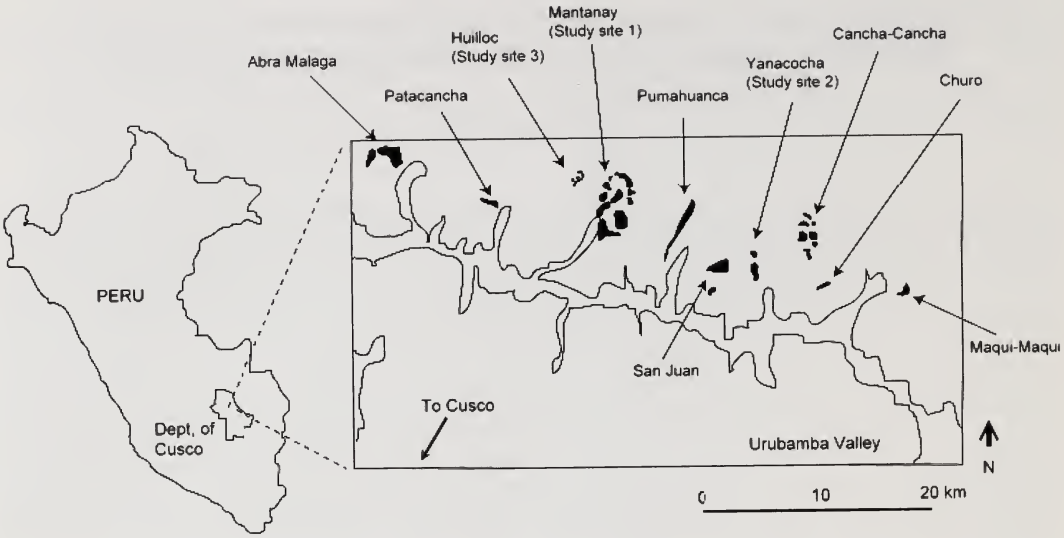


FIG. 1. Schematic showing the main areas of *Polylepis* woodlands, including the three study sites, in the Urubamba Valley, Cordillera Vilcanota, Department of Cusco, southern Peru.

by livestock (Teich et al. 2005), and soil degradation (Renison et al. 2004). These effects combine to prevent forest regeneration, and restrict *Polylepis* woodlands to localized and highly fragmented landscapes (Fjeldså 2002, Kessler 2002). Small remnant patches (<1.0 ha) and scattered trees are a common feature of these landscapes at distances of 30–1,500 m from the larger (>10 ha) patches, and vary in habitat quality (Lloyd and Marsden in press). These patches continue to be eroded due to ongoing firewood collection and burning (Fjeldså and Kessler 1996). Consequently, some *Polylepis* bird species are considered globally-threatened (BirdLife International 2004) and are presumed to have extremely small populations in the tiny forest patches that remain (Fjeldså 1993). If factors that affect resource partitions in remnant forest patches can be identified, this information could enable biologists to predict with greater accuracy the responses of *Polylepis* birds to further habitat loss and degradation, and provide a link to the mechanisms that could be used for active habitat restoration strategies.

The objectives of this paper are to describe (1) foraging patterns, and (2) guild composition of the insectivorous *Polylepis* bird community in remnant forest patches in the Cordillera Vilcanota, southern Peru.

METHODS

Study Sites.—I recorded the foraging ecology of *Polylepis* bird species at three sites in the Cordillera Vilcanota mountain range (Fig. 1). Mantanay (13° 12′ S, 72° 09′ W) at 3,400–4,500 m elevation, above the village of Yanahuara, is one of the largest areas of *Polylepis racemosa* woodland in the Cordillera Vilcanota. The site was surveyed during 67 field days in July 2003, October 2004, and September 2005. Yanacocha (13° 17′ S, 72° 02′ W), ~3,700–4,500 m elevation, above the village of Huaocari, was surveyed for 28 days in October 2003 and June 2004. Laguna Queuñacocha (13° 12′ S, 72° 10′ W) is a small area of *P. pepei* woodland, ~4,200–4,500 m elevation above the village of Huilloc (hereafter referred to as Huilloc), and was surveyed during 22 field days in December 2003 and July 2004.

Foraging Observations.—*Polylepis* birds were located visually and vocally foraging with or independently of mixed-species flocks in both large (≥10 ha) and small (≤1.0 ha) forest patches. Individual birds of all species were followed opportunistically between 0530 and 1730 hrs for as long as they could be kept in view. Sequential foraging observations for each individual were made using 8 × 42 binoculars, recorded on micro-cassette, and later

transcribed to data sheets. Many individuals of each species were sampled reducing problems associated with pseudoreplication. No more than three consecutive sequences of foraging events were taken of each individual to further limit bias (Morrison 1984, Kratter 1995).

The point of each foraging sequence was marked with colored tape. Variables estimated and recorded at the point of each foraging sequence were species, height above ground, and height below the canopy. Vegetation cover at each marked foraging point was estimated using a sighting tube (James and Shugart 1970) once the bird had moved from view. Terminology and strategy for recording prey-attack maneuvers (Table 1) follows Remsen and Robinson (1990). This scheme recognizes the importance of links between the prey-attack maneuver and substrate used by the bird, and places importance on the position from which the prey-attack-maneuver is launched (Remsen and Robinson 1990, Mac Nally 2000).

Bird Counts.—I examined the influence of bird abundance on foraging ecology by surveying birds at census plots along transects within large and small remnant patches using a point count distance sampling method (Reynolds et al. 1980 as adapted by Jones et al. 1995). Each transect was randomly placed with census stations positioned 150 m from each other (Blake and Karr 1987). I used encounter rates of birds recorded within 50 m of the census stations' central point as a measure of relative abundance. Bird surveys were conducted between 0530 and 1630 hrs and only during hours of suitable weather (i.e., in the absence of snow, rain or strong wind). I was the only recorder for the bird surveys and was familiar with the vocalizations of the region's bird species. I sat quietly for a 5-min 'settling down' period (Bibby et al. 2000) following arrival at each plot, before spending 20 min recording all birds seen and heard. Two replicates of each station were made in each patch size category making a total of 180 point counts (100 in large patches and 80 in small patches). The direction of surveys along transects was rotated in an attempt to minimize any bias associated with variable bird activity at different times of day.

Data Analyses: Guild Composition.—Se-

TABLE 1. Perch type, substrate, and attack maneuver variables used in this study. Prey-attack maneuvers follow Remsen and Robinson (1990).

Perch type	Substrate	Prey-attack maneuver surface	Prey-attack maneuver subsurface
Polylepis alive	Main trunk (+/− moss/lichen)	Perch glean	Probe
Polylepis dead	Primary branches (+/− moss/lichen)	Hang-up glean	Flick (includes bill-sweep/toss)
Escallonia alive	Secondary branches (+/− moss/lichen)	Hang-down glean	Pry
Escallonia dead	Outer-most branches (+/− moss/lichen)	Hang-upside-down glean	Pull
Other tree species alive	Inner-most leaves (nearest to main trunk)	Lunge glean	
Other tree species dead	Outer-most leaves	Reach glean (all reach maneuvers)	
Rock/boulder	Leaf node/calyx	Sally-strike glean	
	Flowers	Sally-hover glean	
	Main trunk + tree resin	Flutter chase	
	Primary branches + tree resin		
	Secondary branches + tree resin		
	Outer-most branches + tree resin		
	Ground litter		
	Moss		
	Lichen		
	Air		

quential observations rather than single point observations are the preferred method for sampling foraging behavior of birds from a large sample of individuals because they have a greater tendency to reveal rare behaviors (Hertz et al. 1976, Eckhardt 1979, Holmes et al. 1979, Moermond 1979, Morrison 1984). I used 30 sequential foraging events as the minimum sample size following Morrison (1984). Twenty-three high Andean bird species were recorded during the surveys for which sufficient sample sizes were collected for 12 species. Two of these 12 species were omitted from further analyses. The Royal Cinclodes (*Cinclodes aricomae*) was observed using the ground or boulders as a perch type and moss or bark-ground litter as substrate and was, therefore, separated from the other bird species by perch type, substrate, and niche position. The Thick-billed Siskin (*Carduelis crassirostris*) was observed feeding on either flowers or seeds of *Polylepis* trees and was not considered to be an insectivore.

I selected 100 random point (individual) foraging maneuvers and 100 sequential foraging maneuvers for each species to examine any possible bias of temporal dependence in sequential observations (e.g., Bell et al. 1990) and tested for significant differences using Mann-Whitney *U*-tests. Only two of 12 species examined had significant differences in foraging height above ground; White-browed Tit-spinetail (*Leptasthenura xenothorax*) ($U = 3{,}576$, $P < 0.05$) and Cinereous Conebill (*Conirostrum cinereum*) ($U = 2{,}373$, $P < 0.001$), and only the Giant Conebill (*Oreomanes fraseri*) had a significant difference ($U = 3{,}621$, $P < 0.01$) in foraging height below the canopy. I attributed these results to chance alone, since only 5% of tests were significant, and included all sequential foraging observations in all subsequent analyses.

I used a hierarchical cluster analysis using χ^2 measures of between-group linkage to group species into distinctive guilds based on frequency use of perch type, substrates, and prey-attack maneuvers for each of the 10 bird species. I defined guild as a group of species (>1) that exploit the same class of environmental resources in a similar way (Root 1967, Morrison and Hall 2003). Guilds were assigned by visual inspection of the dendrogram since currently no statistical precedent exists for quantitative separation of species into guilds (Holmes et al. 1979). Differences in foraging (niche) position between species in each guild were examined using Mann-Whitney *U* and Kruskal-Wallis tests. Differences in frequency of use of each perch type, substrate, and prey-attack maneuver between species in each guild were examined with χ^2 tests.

Standardized residuals in contingency tables were analysed to learn whether birds foraged disproportionately at certain perch types or substrates, or disproportionately used certain prey-attack maneuvers (Kratter 1995, Gabbe et al. 2002, Hartung and Brawn 2005). Sequential Bonferroni adjustments of *P* values for overall χ^2 values were not made because they are considered over-conservative with little consensus as to their application for ecological studies (Cabin and Mitchell 2000, Moran 2003, Driscoll and Wier 2005).

Comparison of Foraging Regimes in Different Patch Size Categories.—Eight bird species were selected for analysis based on a minimum sample size of 50 foraging sequences in each patch size category. Twenty random samples of niche position, substrate use, and prey-attack manoeuvres for each of the eight species in both large and small patches were selected. I defined niche position as mean ± SD foraging height range (foraging height above ground and foraging height below canopy). I used J′ evenness scores to examine whether a significant shift in foraging regimes occurs for each species (e.g., Morse 1971, Yeaton 1974) within each guild between large and small patches. I calculated J′ evenness scores of total number and frequency of use of perch types, substrates, and prey-attack maneuvers as measurements of niche breadth, substrate breadth and breadth of prey-attack maneuvers, and tested for significant differences using Mann-Whitney *U*-tests.

Influence of Bird Abundance on Foraging Regimes.—Spearman's rank correlation analyses were used to examine the influence of bird abundance on foraging regimes. I examined the relationship between density shift of each species between large and small patches (abundance in large patches minus abundance in small patches) with the difference in richness and breadth of both substrates and prey-attack maneuvers. I then examined the relationship of species tolerance of small patches

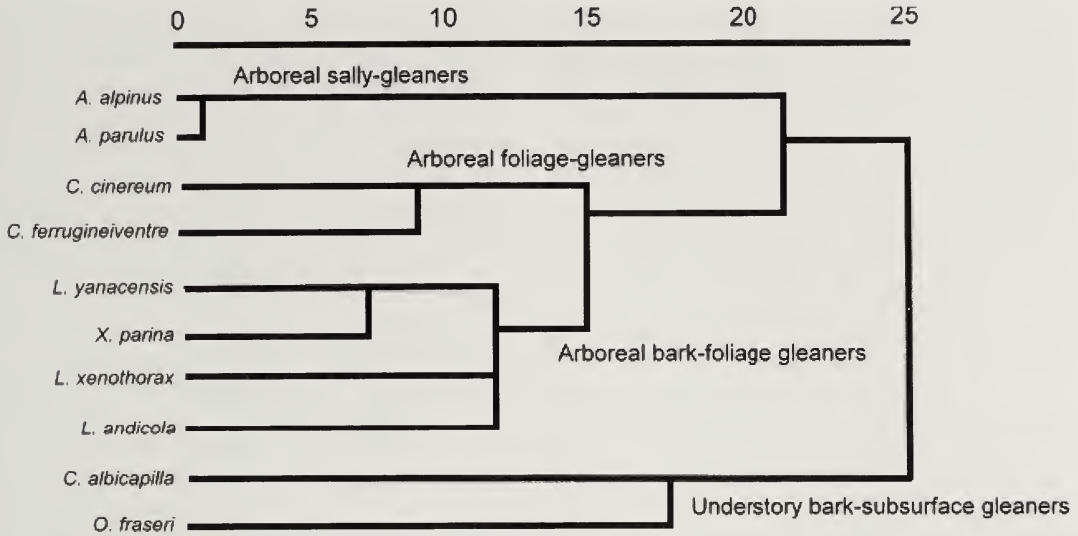


FIG. 2. Hierarchical cluster analysis with dendrogram (using χ^2 measures of between-group linkage) of guild composition of 10 species of insectivorous bird species in *Polylepis* forests based on percent (0–25) use of perch types, substrate, and attack maneuvers.

with differences in richness and breadth of substrates and prey-attack maneuvers. Species tolerance was defined as species abundance in small patches.

RESULTS

Guild Composition.—Individuals (1,122) of 10 species followed during 110 days in the field corresponded to 8,694 foraging events. Guild 1 (Fig. 2) *arboreal sally-gleaners*, included Ash-breasted Tit-tyrant (*Anairetes alpinus*) and Tufted Tit-tyrant (*A. parulus*) that fed primarily on the inner- and outer-most leaves of live *Polylepis* trees using principally sally-strike and perch glean prey-attack maneuvers. Guild 2, *arboreal foliage gleaners*, included both Cinereous Conebill and White-browed Conebill (*Conirostrum ferrugineiventre*), which fed principally on the outer-most leaves of *Polylepis* trees using mainly hang-up and hang-down prey-attack maneuvers. Guild 3, *arboreal bark-foliage gleaners*, included three *Leptasthenura* Tit-spinetail species and Tit-like Dacnis (*Xenodacnis parina*) that fed on the inner- and outer most branches and foliage using hang-up glean as the dominant prey-attack maneuvers. Guild 4, *understory bark-subsurface gleaners*, included the Creamy-crested Spinetail (*Cranioleuca albicapilla*) and Giant Conebill that fed mainly on the surface and subsurface of trunks and branches in the understory of live *Polylepis* trees using similar surface prey-attack maneuvers, but different subsurface prey-attack maneuvers.

Within-guild Niche Position and Niche Breadth: Arboreal Sally-gleaners.—I found a difference ($P < 0.001$) in niche position and mean foraging vegetation cover between the two *Anairetes* species in this guild (Table 2). The Tufted Tit-tyrant foraged higher above ground and nearer the canopy than the Ash-breasted Tit-tyrant, but had a narrower niche position and niche breadth. The Ash-breasted Tit-tyrant foraged in a narrow range of dense *Polylepis* vegetation.

Arboreal Foliage Gleaners.—There were differences in mean height below the canopy ($P < 0.001$) but not in mean height above ground or mean vegetation cover at foraging sites for both arboreal foliage gleaners (Table 2). The White-browed Conebill had the more narrow niche position in foliage closer to the ground, a more narrow niche breadth, and foraged within a narrow range of dense vegetation cover. The Cinereous Conebill had the more narrow niche position for mean foraging height below the canopy.

Arboreal Bark-foliage Gleaners.—There was a difference ($P < 0.001$) in the niche po-

TABLE 2. Niche position (mean ± SD height variables and vegetation cover) and niche breadth (J' Evenness scores) of four insectivorous *Polylepis* guilds. Kruskal-Wallis and Mann-Whitney tests were used to examine within-guild differences between variables.

Guild composition	Number of foraging bouts	Mean ± SD height above ground	Mean ± SD height below canopy	Mean ± SD vegetation cover	Niche breadth
Arboreal sally gleaners					
Anairetes alpinus	401	3.45 ± 1.92	1.71 ± 1.30	76.7 ± 15.8	0.944
A. parulus	384	3.86 ± 1.45	1.28 ± 1.23	71.2 ± 17.2	0.834
		$Z = 14.79$, $P < 0.001$	$Z = -5.77$, $P < 0.001$	$Z = -5.40$, $P < 0.001$	
Arboreal foliage gleaners					
Conirostrum cinereum	723	5.14 ± 2.72	1.42 ± 1.15	70.7 ± 13.6	0.943
C. ferrugineiventre	928	4.95 ± 2.51	2.19 ± 1.85	73.0 ± 10.1	0.835
		$Z = 0.66$, $P = 0.507$	$Z = -7.40$, $P < 0.001$	$Z = 1.82$, $P = 0.068$	
Arboreal bark-foliage gleaners					
Leptasthenura xenothorax	1,361	4.84 ± 2.34	2.05 ± 1.60	73.7 ± 12.6	0.919
L. yanacensis	839	2.98 ± 1.85	1.68 ± 1.28	72.6 ± 16.6	0.841
L. andicola	381	1.70 ± 0.67	1.36 ± 0.79	54.5 ± 19.9	0.852
Xenodacnis parina	628	3.56 ± 1.80	2.00 ± 1.57	71.3 ± 15.4	0.985
		$\chi^2_3 = 813$, $P < 0.001$	$\chi^2_3 = 39.8$, $P < 0.001$	$\chi^2_3 = 189.1$, $P < 0.001$	
Understory bark-subsurface gleaners					
Cranioleuca albicapilla	1,029	4.59 ± 2.39	3.10 ± 2.03	71.2 ± 12.8	0.808
Oreomanes fraseri	2,020	5.31 ± 2.54	2.73 ± 1.59	71.6 ± 15.1	0.838
		$Z = -5.17$, $P < 0.001$	$Z = -9.57$, $P < 0.001$	$Z = -6.68$, $P < 0.001$	

sition and mean vegetation cover between all four species in this guild (Table 2). The White-browed Tit-spinetail and Tit-like Dacnis foraged higher above the ground and lower below the canopy and occupied a wider niche position within the guild. The Andean Tit-spinetail (*Leptasthenura andicola*) foraged lower to the ground than any other species in the guild and also had the more narrow niche position. The White-browed Tit-spinetail foraged within a narrow range of dense *Polylepis* vegetation while the Andean Tit-spinetail foraged in a wider range of more open *Polylepis* vegetation. The Tawny Tit-spinetail (*L. yanacensis*) had the narrowest and Tit-like Dacnis had the widest niche breadth of all four species in the guild.

Understory Bark-subsurface Gleaners.—I detected a difference ($P < 0.001$) in niche position and mean foraging vegetation cover for the two species in this guild (Table 2). The Giant Conebill foraged higher above ground and higher in trees than the Creamy-crested Spinetail. The SD for niche position above the ground was similar for both species but the Giant Conebill occupied a wider niche position below the canopy and also foraged in a narrow range of dense *Polylepis* vegetation cover. The Creamy-crested Spinetail had the more narrow niche breadth of the two species in the guild.

Within-guild Substrate Specialization: Arboreal Sally-gleaners.—There was a difference in the percent use of perch types ($P < 0.01$), substrates ($P < 0.001$), and surface prey-attack maneuvers ($P < 0.001$) between the two species in the guild. The Tufted Tit-tyrant used *Polylepis* trees exclusively as a perch type for all foraging maneuvers. Both *Anairetes* species used a high percent of outermost leaves but the Ash-breasted Tit-tyrant used more types of substrates than its congener. The Ash-breasted Tit-tyrant used hang-up glean in addition to all other prey-attack maneuvers used by the Tufted Tit-tyrant and foraged disproportionately more frequently on inner-most leaves, using the sally-strike glean maneuver disproportionately more frequently. The reverse was apparent for the Tufted Tit-tyrant use of substrates and prey-attack maneuvers.

Arboreal Foliage Gleaners.—There was a difference in the percent use of perch types ($P < 0.001$), substrates ($P < 0.001$), and surface prey-attack maneuvers ($P < 0.001$) between the two species composing this guild. The Cinereous Conebill used leaf node foraging substrates disproportionately more frequently than expected. The White-browed Conebill used a high percent of outermost leaves disproportionately more frequently than expected and, overall, used more substrates and surface prey-attack maneuvers than its congener. The Cinereous Conebill used hang-down glean maneuver disproportionately more frequently than did the White-browed Conebill.

Arboreal Bark-foliage Gleaners.—There was a difference in use of perch types ($P < 0.001$), substrates ($P < 0.001$), and prey-attack maneuvers ($P < 0.001$) by all species within the guild. *Polylepis* trees were the dominant perch type used by all species within the guild, but only the Andean Tit-spinetail used this exclusively as a perch type. The White-browed Tit-spinetail foraged disproportionately more frequently on outer-most branches. The Tawny Tit-spinetail used a greater number of foraging substrates, in particular a high percent of outer-most leaves, and foraged disproportionately more frequently on secondary branches. The Andean Tit-spinetail and Tit-like Dacnis foraged disproportionately more frequently on inner-most leaves. The Tit-like Dacnis used the greatest number of prey-attack maneuvers. All three *Leptasthenura* species used a higher percent of hang-up glean surface prey-attack maneuvers than the Tit-like Dacnis. Both White-browed and Andean Tit-spinetails used the hang-upside-down-glean maneuver disproportionately more frequently than other prey-attack maneuvers, whereas the Tawny Tit-spinetail used hang-up, and the Tit-like Dacnis used perch glean disproportionately more frequently than expected.

Understory Bark-subsurface Gleaners.—There was a difference in the use of perch types ($P < 0.001$), substrates ($P < 0.001$), surface ($P < 0.001$), and subsurface prey-attack maneuvers ($P < 0.001$) between the two species in the guild. Only the Giant Conebill used *Polylepis* trees exclusively as perch types. The Creamy-crested Spinetail used a high percent of secondary branches and foraged disproportionately more frequently on secondary branch lichen. The Giant Conebill used a

higher percent than the Creamy-crested Spinetail and foraged disproportionately more frequently on the main trunk substrate. The Creamy-crested Spinetail used the hang-up-side-down glean attack maneuver disproportionately more frequently than the Giant Conebill.

Foraging Regimes in Large vs. Small Patches: Arboreal Sally-gleaners.—There were insufficient samples for the Ash-breasted Tit-tyrant in both forest patch size categories for the species to be included in the analysis. The Tufted Tit-tyrant foraged higher ($P < 0.05$) above ground and used a wider range of vertical foraging heights above the ground ($P < 0.001$) in large patches. The Tufted Tit-tyrant foraged in small patches in more dense vegetation cover ($P < 0.001$) and in a more narrow range of more dense vegetation cover ($P < 0.001$). Richness and breadth of prey-attack maneuvers used by the Tufted Tit-tyrant were greater in small patches, and differed ($P < 0.001$) between both patch size categories.

Arboreal Foliage-gleaners.—The niche position for White-browed and Cinereous conebills differed ($P < 0.001$) between large and small patches. Both species foraged higher above ground ($P < 0.001$) and in more dense vegetation cover ($P < 0.05$) in large patches. The Cinereous Conebill foraged significantly further from the canopy ($P < 0.001$) in large patches while the reverse was apparent for the White-browed Conebill. Richness and breadth of substrates used by both guild members differed ($P < 0.001$) between large and small patches. There was a difference in the richness ($P < 0.001$) and breadth of attack maneuvers ($P < 0.001$) between large and small patches by both guild members.

Arboreal Bark-foliage Gleaners.—There were insufficient samples for the Andean Tit-spinetail in both patch size categories for it to be included in the analysis. The niche position for the remaining three guild members differed ($P < 0.001$) between large and small patches. The White-browed Tit-spinetail foraged higher above ground ($P < 0.001$) and in more dense vegetation ($P < 0.001$) in large patches than in small patches. Both the Tawny Tit-spinetail and Tit-like Dacnis foraged higher above ground ($P < 0.01$ and $P < 0.001$, respectively) and closer to the canopy ($P < 0.001$) in large patches, but foraged in more dense vegetation cover ($P < 0.001$) and across a more narrow range of dense vegetation cover ($P < 0.001$) in small patches.

Overall richness and breadth of substrates used by both the White-browed and Tawny tit-spinetails differed ($P < 0.001$) between large and small patches. Both substrate richness and substrate breadth used by Tit-like Dacnis differed ($P < 0.001$) between both patch size categories. There was a difference ($P < 0.001$) in the breadth but not richness of prey-attack maneuvers used by the White-browed Tit-spinetail. There was a difference ($P < 0.001$) in richness but not breadth of prey-attack maneuvres by the Tawny Tit-spinetail between large and small patches. Richness and breadth of attack maneuvers used by the Tit-like Dacnis were greater in large patches and differed ($P < 0.001$) between large and small patches.

Understory Bark-subsurface Gleaners.—The niche position of the Creamy-crested Spinetail and Giant Conebill differed ($P < 0.001$) between large and small patches. Both species foraged higher above ground ($P < 0.001$) and closer to the canopy ($P < 0.001$) in large patches, and foraged in more dense vegetation ($P < 0.001$) and in a more narrow range of dense vegetation cover ($P < 0.001$) in small patches. Richness but not breadth of substrates used by the Creamy-crested Spinetail differed ($P < 0.001$) between both patch size categories. Overall richness and breadth of substrates used by the Giant Conebill differed ($P < 0.001$) between large and small patches. There was a difference ($P < 0.001$) in use of both surface and subsurface prey-attack maneuvers between large and small patches by both guild members. Overall richness and breadth of prey-attack maneuvers used by the Creamy-crested Spinetail were greater in large patches and differed ($P < 0.001$) between both patch size categories. There was a difference ($P < 0.001$) in richness but not breadth of prey-attack maneuvers used by the Giant Conebill between both patch size categories.

Bird Abundance and Foraging Regimes.—There was a significant negative correlation ($r^2 = -0.89$, $P < 0.01$) between the shift in species density and the richness of prey-attack maneuvers used by insectivores in small patches, suggesting the most abundant of the eight focal species (both arboreal foliage

gleaners) were the least diverse foragers, using fewer attack maneuvers in small patches. A significant positive correlation ($r^2 = 0.74$, $P < 0.05$) between species tolerance in smaller patches and difference in the breadth of substrates used indicated that species which demonstrated a significant shift in foraging regimes to use fewer substrates in smaller patches, all fairly frequently (Cinereous Conebill, Tawny Tit-spinetail, and Giant Conebill), were more tolerant of small patches. There was a significant negative correlation ($r^2 = -0.81$, $P < 0.05$) between species tolerance and the difference in the richness of prey-attack maneuvers in small patches. Species demonstrated a significant shift of their foraging regime using fewer prey-attack maneuvers (Cinereous Conebill, Tawny Tit-spinetail, and Giant Conebill) were more tolerant of small patches (Table 3). Species that continued to use many different prey-attack maneuvers, and some only rarely (i.e., having a more inflexible, or rigid foraging regime [White-browed Conebill and Tufted Tit Tyrant]), were least tolerant of small forest patches (Table 3).

TABLE 3. Changes in foraging regimes of eight insectivorous *Polylepis* bird species between large and small patches. * Significant difference between large and small patches.

Guild	Species	Shift in foraging regimes from large to small patches
Arboreal sally gleaners	*Anairetes parulus*	Shift to foraging lower, in more dense and in narrower range of vegetation cover *
		Shift to use different breadth of prey-attack maneuvers *
		Uses similar breadth of substrates
Arboreal foliage-gleaners	*Conirostrum cinereum*	Shift to foraging lower, in more dense vegetation cover *
	C. ferrugineiventre	Shift to use different breadth of substrates and prey-attack maneuvers *
Arboreal bark-foliage-gleaners	*Leptasthenura xenothorax*	Shift to foraging lower, in more dense and in narrower range of vegetation cover *
	L. yanacensis	Shift to use different breadth of substrates and prey-attack maneuvers *
	Xenodacnis parina	

DISCUSSION

Guild Composition and Resource Partitioning.—A number of distinctive guilds were identified within the insectivorous bird community in *Polylepis* forests based on relatively few foraging parameters. These guilds partition resources by selecting differences in niche position (range of foraging heights), density (and range) of vegetation cover, frequency of substrate use, and prey-attack maneuvers. The important dimensions that enabled differentiation among guild members were similar to those that support partitioning of resources between guilds. The organization of insectivorous *Polylepis* bird communities can be understood largely in terms of where species forage in relation to tree height, vegetation cover, substrate use, and prey-attack maneuvers. Studies of temperate forest insectivorous bird communities have yielded similar conclusions (e.g., MacArthur and MacArthur 1961, Recher 1969, Holmes et al. 1979, Vassallo and Rice 1982, Gabbe et al. 2002).

Ecological separation of insectivorous bird species is not unexpected. In areas of high habitat-restricted endemism, such as the Cor-

dillera Vilcanota *Polylepis* forests, one would expect to find bird species with leptokurtic niche positions (i.e., bird species are specialized to compete for fairly predictable food resources) (e.g., Stenseth 1980). What is unclear from the analyses, however, is whether the niche position of insectivorous high Andean birds in remnant patches is either leptokurtic or platykurtic (i.e., whether each bird species is trying to monopolize a certain part of the habitat). I cannot be sure how representative these results are of other fragmented *Polylepis* landscapes because this study was confined to only three sites in the Cordillera Vilcanota. Some of the focal bird species differ markedly in their ecological amplitude in different habitats (e.g., Cinereous Conebill, Tufted Tit-tyrant) and this study covers only a fraction of their full ecological range.

Substrate Specialization.—The significant disproportionate use of substrates and prey-attack maneuvers indicates substrate specialization within the insectivorous *Polylepis* bird community. *Polylepis* trees differ in the proportion of branches and vegetation cover at different heights (Fjeldså and Kessler 1996). These differences may affect many of the substrate foraging opportunities and constraints for *Polylepis* birds. Similar differences are known to influence the foraging ecology of temperate forest insectivores (e.g., Holmes and Recher 1986, Cueto and Casenave 2002, Lyons 2005) in combination with richness and abundance of prey species in different foliage or branching compartments (Holmes and Robinson 1981, Rosenberg 1993). Consequently, variation in *Polylepis* vegetation structure could provide a number of opportunities to increase substrate specialization, enabling species to partition resources along these axes, possibly leading to a relaxation of between- and within-guild competitive pressures.

This hypothesis is supported by the presence of the Andean Tit-spinetail foraging within the same forest patches as the White-browed Tit-spinetail. Previously, these species were thought not to occur in the same *Polylepis* woodlands (Fjeldså and Krabbe 1990) and rarely in Peru do two of the streaked-plumaged *Leptasthenura* species occur syntopically (Fjeldså and Krabbe 1990). My findings show that closely related *Leptasthenura* species are able to occur syntopically and partition resources principally on the disproportionate use of different perch types, substrates, and differences in the range of foraging heights and vegetation cover (niche position). Similar disproportionate use of understory substrates, and differences in foraging heights are important factors promoting increased substrate specialization among numerous neotropical lowland insectivores such as *Myrmotherula* antwrens that habitually follow mixed-species flocks (e.g., Gradwohl and Greenberg 1984, Remsen and Parker 1984, Rosenberg 1993), and species restricted to *Guadua* bamboo habitats (Kratter 1995).

Shift in Foraging Regimes.—*Polylepis* insectivores demonstrated differential response to foraging in smaller patches; changes in the foraging regimes used by members of the four guilds between large and small patches were frequent (Table 3). Similar results have been found among temperate forest bird species, most noticeably the well studied *Parus* genus (e.g., Krebs et al. 1972, Partridge 1976, Alatalo 1982) and between island and mainland passerine bird populations (Yeaton 1974). This suggests that High-Andean insectivorous guilds are able to respond behaviorally to some habitat loss and alteration. The shifts in foraging regimes are significant because small *Polylepis* patches differed from larger patches at all sites in habitat quality (i.e., small patches had greatly reduced tree density, contained smaller, shorter trees, and a wider range of more open canopy vegetation cover, than larger patches) (Lloyd 2007). Some authors have suggested that differences in habitat quality of forest patches are a proximate cause of the shift in foraging regimes for temperate forest-dependent bird species (e.g., Morse 1971, Franzeb 1978, Maurer and Whitmore 1981).

Factors such as habitat quality are unlikely to act in isolation (Wiens 1989, Jedlicka et al. 2006). The Spearman's rank correlation analyses indicate the combined effects of habitat quality with changes in bird abundance between large and small patches also exerts a significant influence on variation in *Polylepis* bird foraging regimes. The most abundant *Polylepis* insectivores in small patches were the least diverse foragers and compensated behaviorally by opportunistically using fewer substrates and prey-attack maneuvers with similar frequency. Insectivores that shifted their for-

aging regime to use fewer prey-attack maneuvers were also more tolerant of small patches. Shifts in foraging regimes may also be explained by the combined effects of variation in habitat quality with changes in area-dependent or disturbance-related prey resources (e.g., González-Gomez et al. 2006, Jedlicka et al. 2006), or with differences in microclimate conditions (Cahill and Matthysen 2007), but such data are lacking from the Cordillera Vilcanota.

Five species from three guilds (Tufted Tit-tyrant, Tawny Tit-spinetail, Tit-like Dacnis, Creamy-crested Spinetail, and Giant Conebill) significantly altered their foraging regime to forage at a significantly lower height, use a more narrow range of foraging heights, and foraged within a more narrow range of denser vegetation cover (Table 3). These responses could be a proportional measure to foraging in smaller, shorter trees. Alternatively, these species could be accommodating for a shift in the perception of predation risk by raptors (e.g., *Glaucidium* Pygmy-owl species, Herzog et al. 2003) in smaller patches. Habitat loss and alteration has an important role in shaping the effect of changing predation risk on the behavioral responses of birds in fragmented landscapes (Lima et al. 1987, Zollner and Lima 2005, Cahill and Matthysen 2007). Temperate forest insectivores foraging in small patches spend more time foraging in dense canopy cover and significantly increase their scanning and hopping rates (Pulliam and Mills 1977, Telleria et al. 2001). Similar time-budget analysis of *Polylepis* bird foraging rates between large and small patches would prove invaluable in future studies.

IMPLICATIONS FOR *POLYLEPIS* CONSERVATION

Research from Bolivia has suggested that small *Polylepis* forest patches with large edges will probably not provide suitable habitat for *Polylepis* habitat specialists (Cahill and Matthysen 2007). The results from my study suggest that small *Polylepis* patches are part of a wider, High-Andean landscape mosaic, and have a significant role in fragmented *Polylepis* ecosystem functioning by providing suitable foraging habitat for insectivorous birds. Small patches should not be excluded from habitat restoration strategies. Strategies that use small patches as a starting point are more likely to be implemented in the short term than larger scale projects due to lower costs (e.g., Fenton 1997, Fischer and Lindenmayer 2002). Maintenance and expansion of small patches across the Cordillera Vilcanota landscape should focus on maximizing features of within-patch habitat quality such as high density of small trees with dense vegetation cover. Maintaining these critical vegetation components will promote a greater tolerance of small patches by insectivores and provide the necessary conditions for microhabitat use and resource partitioning amongst insectivorous guilds. This could increase the functional connectivity of threatened bird populations.

Polylepis regeneration naturally happens mainly at forest edges, where there are higher densities of seedlings (Cierjacks et al. 2007), but these areas are usually destroyed by extensive burning and grazing by livestock. Future landscape management strategies must require a more sympathetic approach to reducing the dependency by local communities on traditional land-use patterns of firewood extraction, intense grazing by livestock, and pasture burning in and around small patches and forest edges.

ACKNOWLEDGMENTS

Barry and Rosario Walker of Manu Expeditions, and the Department of Environmental and Geographical Sciences, Manchester Metropolitan University, sponsored the research. I thank Constantino Aucca and ECOAN, Eliana Manga, Freddy Padovani, Navidad Abandanio, Mary Montesinos, the Department of Immigration (Cusco Region, Peru) and the Peruvian Consulate in London for their help and support. Stuart Marsden, Alan Fielding, Luc Lens, and two anonymous reviewers greatly improved the manuscript.

LITERATURE CITED

Alatalo, R. 1982. Multi-dimensional foraging niche organization of foliage-gleaning birds in northern Finland. Ornis Scandinavica 13:56–71.

Bell, G. W., S. J. Hejl, and J. Verner. 1990. Proportional use of substrates by foraging birds: model considerations on first sightings and subsequent observations. Studies in Avian Biology 13:161–165.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. Bird census techniques. Second Edition. Academic Press, London, United Kingdom.

BirdLife International. 2004. Threatened birds of

the world 2004. CD-ROM. BirdLife International, Cambridge, United Kingdom.

Blake, J. G. and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724–1734.

Cabin, R. J. and R. J. Mitchell. 2000. To Bonferroni or not to Bonferroni: when and how are the questions. Bulletin of the Ecological Society of America 81:246–248.

Cahill, J. R. A. and E. Matthysen. 2007. Habitat use by two specialist birds in High-Andean *Polylepis* forests. Biological Conservation 140:62–69.

Capriles, J. M. and E. Flores. 2002. The economic, symbolic and social importance of the "Queñua" (*Polylepis* spp.) during pre-Hispanic times in the Andean highlands of Bolivia. Ecotropica 8:225–231.

Cierjacks, A., J. E. Iglesias, K. Wesche, and I. Hensen. 2007. Impact of sowing, canopy cover and litter on seedling dynamics of two *Polylepis* species at upper tree lines in central Ecuador. Journal of Tropical Ecology 23:309–318.

Cueto, V. R. and J. L. de Casenave. 2002. Foraging behavior and microhabitat use of birds inhabiting coastal woodlands in east-central Argentina. Wilson Bulletin 114:342–348.

Diamond, J. M., K. D. Bishop, and S. van Balen. 1987. Bird survival in an isolated Javan woodland: island or mirror? Conservation Biology 1: 132–142.

Driscoll, D. A. and T. Weir. 2005. Beetle responses to habitat fragmentation depend on ecological traits, remnant condition and shape. Conservation Biology 19:182–194.

Eckhardt, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. Ecological Monographs 49: 129–149.

Ellenberg, H. 1958. Wald oder Steppe? Die naturliche Pflanzendecke der Anden Perus. Umschau in Wissenschaft und Technik 21:645–681.

Fæth, S. H. and T. C. Kane. 1978. Urban biogeography: city parks as islands for Diptera and Coleoptera. Oecologia 32:127–133.

Fenton, J. 1997. A primary producer's perspective on nature conservation. Pages 3–9 *in* Conservation outside nature reserves (P. Hale and D. Lamb, Editors). University of Queensland, Brisbane, Australia.

Fischer, J. and D. B. Lindenmayer. 2002. The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones. Biodiversity and Conservation 11:833–849.

Fischer, J., I. Fazey, R. Briese, and D. B. Lindenmayer. 2005. Making the matrix matter: challenges in Australian grazing landscapes. Biodiversity and Conservation 14:561–578.

Fjeldså, J. 1992. Evolution of the avifauna inhabiting woodlands isolated on very high altitudes in the Andes. Steenstrupia 18:9–62.

Fjeldså, J. 1993. The avifauna of the *Polylepis* woodlands of the Andean highlands: the efficiency of basing conservation priorities on patterns of endemism. Bird Conservation International 3:37–55.

Fjeldså, J. 2002. *Polylepis* forests—vestiges of a vanishing ecosystem in the Andes. Ecotropica 8:111–123.

Fjeldså, J. and M. Kessler. 1996. A strategy for conserving the biological diversity of *Polylepis* woodlands of the High Andes in Peru and Bolivia. CTB/NORDECO, Copenhagen, Denmark.

Fjeldså, J. and N. Krabbe. 1990. Birds of the High Andes. Zoological Museum and Apollo Books, Copenhagen and Stenstrup, Denmark.

Franzeb, K. E. 1978. Tree species used by birds in logged and unlogged mixed-coniferous forest. Wilson Bulletin 90:221–238.

Gabbe, A. P., S. K. Robinson, and J. D. Brawn. 2002. Tree-species preferences of foraging insectivorous birds: implications for floodplain forest restoration. Conservation Biology 16:462–470.

González-Gómez, P. L., C. F. Estades, and J. A. Simonetti. 2006. Strengthened insectivory in a temperate fragmented forest. Oecologia 148:137–143.

Gradwohl, J. and R. Greenberg. 1984. Search behaviour of the Checker-throated Antwren foraging in aerial leaf-litter. Behavioural Ecology and Sociobiology 15:281–285.

Guevara, S. and J. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Vegetatio 107/108:319–338.

Hartung, S. and J. D. Brawn. 2005. Effects of savanna restoration on the foraging ecology of insectivorous birds. Condor 107:879–888.

Hertz, P. E., J. V. Remsen, and S. I. Jones. 1976. Ecological complementarity of three sympatric parids in a California oak woodland. Condor 78: 307–316.

Herzog, S. K., A. R. Soria, and E. Matthysen. 2003. Seasonal variation in avian community composition in a High-Andean *Polylepis* (Rosaceae) forest fragment. Wilson Bulletin 115:438–447.

Herzog, S. K., A. R. Soria, A. Troncoso, and E. Matthysen. 2002. Composition and structure of avian mixed-species flocks in a High-Andean *Polylepis* forest in Bolivia. Ecotropica 8:133–143.

Holmes, R. T. and H. F. Recher. 1986. Determinants of guild structure in forest bird communities: an intercontinental comparison. Condor 88:427–439.

Holmes, R. T. and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31–35.

Holmes, R. T., R. E. Bonney, and S. W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60: 512–520.

Jaenike, J. 1978. Effect of island area on *Drosophila* population densities. Oecologia 36:327–332.

James, F. C. and H. H. Shugart Jr. 1970. A quanti-

tative method of habitat description. Audubon Field Notes 24:727–736.

Jedlicka, J. A., R. Greenberg, I. Perfecto, S. M. Philpott, and T. V. Dietsch. 2006. Seasonal shift in the foraging niche of a tropical avian resident: resource competition at work? Journal of Tropical Ecology 22:385–395.

Jones, M. J., M. D. Lindsey, and S. J. Marsden. 1995. Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia. Bird Conservation International 5:21–52.

Kessler, M. 2002. The "*Polylepis* problem": where do we stand? Ecotropica 8:97–110.

Kratter, A. W. 1995. Bamboo specialization in Amazonian birds. Dissertation. Louisiana State University, Baton Rouge, USA.

Krebs, J. R., M. H. MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the Great Tit *Parus major*: an experimental study. Ibis 114:507–530.

Lima, S. L., K. L. Wiebe, and L. M. Dill. 1987. Protective cover and the use of space by finches—is closer better? Oikos 50:225–230.

Lloyd, H. 2007. Abundance and ecology of High-Andean *Polylepis* birds in Perú: implications for habitat management strategies. Dissertation. Manchester Metropolitan University, Manchester, United Kingdom.

Lloyd, H. and S. J. Marsden. In press. Bird community variation across *Polylepis* woodland fragments and matrix habitats: implications for conservation within a High Andean landscape. Biodiversity and Conservation: In press.

Lyons, J. E. 2005. Habitat-specific foraging of Prothonotory Warblers: deducing habitat quality. Condor 107:41–49.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

Mac Nally, R. 2000. Coexistence of a locally undifferentiated foraging guild: avian snatchers in a southeastern Australian forest. Austral Ecology 25:69–82.

Manning, A. D., J. Fischer, and D. B. Lindenmayer. 2006. Scattered trees are keystone structures—implications for conservation. Biological Conservation 132:311–321.

Maurer, B. A. and R. C. Whitmore. 1981. Foraging of five bird species in two forests with different vegetation structure. Wilson Bulletin 93:478–490.

Moermond, T. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. Ecology 60:152–164.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403–405.

Morrison, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. Condor 86:146–150.

Morrison, M. L. and L. S. Hall. 2003. Standard terminology: toward a common language to advance ecological understanding and application. Pages 43–52 *in* Predicting species occurrences: issues of accuracy and scale (J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, Editors). Island Press, Washington, D.C., USA.

Morse, D. H. 1971. The foraging of warblers isolated on small islands. Ecology 52:216–228.

Mulhlenberg, M., D. Leipold, H. J. Mader, and B. Steinhauer. 1977. Island ecology of arthropods. 2. Niches and relative abundances of Seychelles ants (Formicidae) in different habitats. Oecologia 29:117–134.

Partridge, L. 1976. Field and laboratory observations on the foraging and feeding techniques of Blue Tits (*Parus caeruleus*) and Coal Tits (*P. ater*) in relations to their habitat. Animal Behaviour 24: 534–544.

Pulliam, H. R. and G. S. Mills. 1977. The use of space by wintering sparrows. Ecology 58:1393–1399.

Recher, H. F. 1969. Bird species diversity and habitat diversity in Australia and North America. American Naturalist 103:75–80.

Remsen, J. V. and T. A. Parker. 1984. Arboreal dead-leaf-searching birds of the Neotropics. Condor 86: 36–41.

Remsen, J. V. and S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Studies in Avian Biology 13: 144–160.

Renison, D., A. M. Cingolani, and R. Suarez. 2002. Effects of fire on a *Polylepis australis* (Rosaceae) woodland in the mountains of Cordoba, Argentina. Revista Chilena de Historal Natural 75:719–727.

Renison, D., I. Hensen, and A. M. Cingolani. 2004. Anthropogenic soil degradation affects seed viability in *Polylepis australis* mountain forests of central Argentina. Forest Ecology and Management 196:327–333.

Renison, D., I. Hensen, R. Suarez, and A. M. Cingolani. 2006. Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence? Journal of Biogeography 33:876–887.

Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecological Monographs 37:317–350.

Rosenberg, K. V. 1993. Diet selection in Amazonian antwrens: consequences of substrate specialization. Auk 110:361–375.

Stenseth, N. C. 1980. Spatial heterogeneity and population stability: some evolutionary consequences. Oikos 35:165–184.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker, and D. K. Moskovits. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Teich, I., A. M. Cingolani, D. Renison, I. Hensen,

AND M. A. GIORGIS. 2005. Do domestic herbivores retard *Polylepis australis Bitt.* woodland recovery in the mountains of Cordoba, Argentina? Forest Ecology and Management 219:229–241.

TELLERIA, J. L., E. VIRGÓS, R. CARBONELLI, J. PÉREZ-TRIS, AND T. SANTOS. 2001. Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. Oikos 95:253–264.

VASSALLO, M. I. AND J. C. RICE. 1982. Ecological release and ecological flexibility in habitat use and foraging of an insular avifauna. Wilson Bulletin 94:139–155.

WIENS, J. A. 1989. The ecology of bird communities. 1. Foundations and patterns. Cambridge University Press, Cambridge, United Kingdom.

YEATON, R. I. 1974. An ecological analysis of chaparral and pine forest bird communities on Santa Cruz Island and mainland California. Ecology 55: 959–973.

ZOLLNER, P. A. AND S. L. LIMA. 2005. Behavioural tradeoffs when dispersing across a patchy landscape. Oikos 108:219–230.

The Wilson Journal of Ornithology 120(3):545–549, 2008

NESTING BIOLOGY OF THE GIANT CONEBILL (*OREOMANES FRASERI*) IN THE HIGH ANDES OF BOLIVIA

J. R. A. CAHILL,[1,2,3] E. MATTHYSEN,[2] AND N. E. HUANCA[1]

ABSTRACT.—Eight nests of the Giant Conebill (*Oreomanes fraseri*, Family Thraupidae) were found in *Polylepis* forest fragments in Cochabamba Department (Sacha Loma and Cuturi) of Bolivia during 2002–2004. The breeding period of the Giant Conebill extended from September to December at the beginning of the rainy season. The nests were open cups with an average outside width of 20 cm and a thick rim of 5.5 cm; the average clutch size was 1.86. Nests were constructed mostly with parts of *Polylepis* trees and a variety of mosses. All nests located were in the interior of forests, well camouflaged, and in trees with an average height of 3.16 m. Control of human disturbance, especially burning, is needed for protection of the habitat of the Giant Conebill. *Received 24 April 2007. Accepted 17 October 2007.*

The Giant Conebill (*Oreomanes fraseri*) is in a monotypic genus of the Thraupidae and occurs patchily (Vuilleumier 1984) in the Andes from Colombia to Argentina and Chile (Salaberry et al. 1992, Fjeldså and Kessler 1996, Mazar Barnett et al. 1998). This species is a true specialist of Quewiña (*Polylepis*, Rosaceae) forest (Fjeldså and Krabbe 1990, Fjeldså 2002), which is now highly fragmented and degraded (Ridgely and Tudor 1989, Fjeldså and Kessler 1996, Kessler 2002). The progressive disappearance of *Polylepis* forests has led to the Giant Conebill's occurrence in isolated forest fragments (Fjelså and Kessler 1996). It is considered as a near threatened species due to habitat loss and degradation (Birdlife International 2006).

Few studies of the Andean bird fauna give full details of the geographical distribution and taxonomic position of the Giant Conebill (Vuilleumier 1984, Fjeldså and Krabbe 1990, Stotz et al. 1996). González and Torres-Mura (2000) described one well camouflaged and open nest but, overall, there is a lack of studies on the reproductive biology (Isler and Isler 1987) or general ecology of the Giant Conebill. Studies of the nesting biology of other Thraupidae indicate that open cup nests are built by many genera including *Conothraupis*, *Bangsia*, *Conirostrum*, and all *Tangara* species for which nests are known (Robbins and Glenn 1988, Long and Heath 1994, Estades and Lopez-Calleja 1995, Isler and Isler 1999, Greeney et al. 2006). Studies of the reproductive biology and nesting ecology of the monotypic genus *Oreomanes*, the sister genus of *Conirostrum* (Burns et al. 2003), should provide phylogenetically important information on the ecology of the Thraupidae.

We had the opportunity to observe the breeding ecology and nests of *O. fraseri* from 1999 to 2007 during collection of data on the ecology and behavior of the avifauna of Bolivian *Polylepis* forests. Our objectives in this paper are to describe: (1) the nest, and (2) aspects of the nesting ecology of the Giant Conebill.

METHODS

We conducted studies in Quewiña forest fragments in the Tiraque-Vacas mountain range near the villages of Sacha Loma and Cuturi in the Cochabamba Department of Bolivia (17° 44′ S, 65° 34′ W). These forest fragments were among the largest and densest patches of *Polylepis besseri* forest within 60 km of the city of Cochabamba. The fragments were: (A) 32, (B) 34.9, (G) 5.3, and (J) 19.9 ha, respectively, in size within an altitude range of 3,500–3,900 m.

Polylepis besseri (Rosaceae) was the only tree species present (1 to 6 m in height); shrubs of *Berberis* (Berberidaceae), *Ribes* (Grossulariaceae), *Gynoxis* (Asteraceae), *Baccharis* (Asteraceae), and *Brachiotum* (Melastomataceae) comprised 70% of the vegetation structure. Trees taller than 3 m comprised a small part of the vertical structure in most of our study sites (Fragment A: 21%, B: 29%, G: 24%, J: 65%). Forest fragments were embedded in high An-

[1] Centro de Biodiversidad y Genética, Universidad Mayor de San Simón, Casilla 538, Cochabamba, Bolivia.

[2] Evolutionary Ecology Group, University of Antwerp, B-2610, Antwerp, Belgium.

[3] Corresponding author;
e-mail: jcahill@fcyt.umss.edu.bo

dean Puna grassland dominated by *Calamagrostis antoniana* and *Festuca dolicophylla* (Poaceae) (Fernandez et al. 2001).

We found a pair of Giant Conebills during a bird census on 10 October 2002 in Fragment B that were in the last stage of building their nest. We returned on 8 November 2002 and found two chicks, which fledged 1 week later. We then collected the nest for a detailed analysis of its construction and contents. We collected three additional nests during the 2003–2004 rainy period; their structure and materials were also analyzed following Hansell (2000).

We described seven active nests found in the rainy period of 2003–2004, and weighed two eggs from one of the nests, ~4 days before hatching. We monitored these nests once every week until the chicks fledged. Nestlings were weighed and measured (tarsus) 2–3 days before fledging. We recorded the height and diameter of the substrate tree and height of the nest above ground level for each nest. Nests >50 m from the forest's edge were considered to be in the interior of the forest fragment (Cahill and Matthysen 2007).

OBSERVATIONS

Breeding Season and Behavior.—We found one nest with the parents incubating on 30 October 2003 in Fragment A. We found six additional nests in mid November (Fragment A, 2 nests; Fragment C, 1 nest) and early December (Fragment J, 1 nest; Fragment B, 2 nests) during the breeding period. No active nests were found from January to September 2004.

Both parents took turns incubating the eggs. Two young hatched by 5 November and both parents provisioned them. Observations of four of six nests showed that one parent, acting as a sentinel, perched on a high branch of a *Polylepis* tree until the other returned with food, approaching the nest by short flights and jumps between *Polylepis* branches. The parents did not emit songs while approaching the nest or during the provisioning process. Chicks made loud chirps when a parent approached and, when close to fledging, they moved to the edge of the nest rim to be fed. Both parents removed fecal sacs.

Nests.—All nests were open cups (Fig. 1). The external portion of each was composed of twigs and sticks interwoven tightly with soft plant material. Three collected nests had a mean (± SD) mass of 201 ± 44 g with an average external height of 9.5 ± 0.7 cm and an average width of 20 ± 1 cm. The internal egg cup had a diameter of 9 cm and a depth of 5 cm. The bodies of hatchlings were 100% covered within this space.

FIG. 1. Schematic drawing of the nest of the Giant Conebill.

All nests were supported by 3–5 branches of a *Polylepis* tree. Nests were placed within the space surrounded by branches and secured by twigs and grasses. The tree branches of three nests were interwoven tightly with the nest materials and the branches were used as part of the nest structure.

The nest material used consisted mostly of *Polylepis* parts. Additionally, 21 species of plants were used in smaller amounts, 76% of which were mosses (Table 1). The nest had an external layer with a structural and a decorative part. The lower, structural part was composed of twigs, sticks, and grasses. The upper decorative part, which was most visible, was comprised of many types of mosses (densely interwoven), flakes of thin *Polylepis* bark, and *Polylepis* leaves. This layer gave the nest a dark greenish color.

The internal structural layer had *Polylepis* bark strips with finer twigs, some of which were partly covered with small amounts of mud. The nest lining consisted of two parts. The outermost part had mosses, stems of *Cajophora* sp. (Loasacaeae), thin flakes of *Polylepis* bark, and parts of Cyperaceae and Poaceae (roots, heads, and stems). The innermost part, which came in contact with the chicks, contained bird feathers (most likely from tinamou such as *Nothura darwini*) and sheep wool (Table 1).

TABLE 1. Plant materials in the nest of the Giant Conebill in a *Polylepis besseri* forest in Sacha Loma and Cuturi (Cochabamba, Bolivia).

Material	Layer	Species
Twigs and sticks	External and internal structural	*Polylepis besseri*, *Ribes* sp.
Leaves	External decorative	*Polylepis besseri*
Roots	External decorative	*Cyperacea*
Mosses	External decorative	*Neckera complanata*, *Bartramia potosica*, *Papillaria c.f. nigrences*, *Drepanocladus revolvens*, *Neckera andina c.f.*, *Racomitrium crispipilum*, *Hedwigidium integrifolium*, *Syntrichia princeps*, *Bryum andicola*, *Macromitrium* sp., *Lekea* sp., *Breutelia* sp., *Cyclodietyon* sp., *Leptodontium* sp.
	Lining	*Metzgeria* sp., *Frulania* sp.
Grasses	External structural and lining	*Festuca* sp., *Deyeuxia* sp.
Bark	External decorative and internal structural	*Polylepis besseri*
Stems	Lining	*Ribes* sp., *Cajophora horridus*

Nestlings.—One nest found in the incubation stage contained two white eggs with tiny brown specks with a mean (± SD) weight of 3.0 ± 0.2 g. Three of the six nests found in the nesting period had two chicks, two had one chick, and one had three chicks. We found a dead chick shortly after the start of nest monitoring in two of the three nests with two hatchlings. The average mass and tarsus length of chicks at an average age of 13 ± 2 days (n = 11) were 21.01 ± 1.18 g and 21.95 ± 0.94 mm, respectively. Chicks at this stage were close to fledging since most pin feathers had become feathered. The young (n = 11) fledged 14–16 days after hatching. Fledglings had a conspicuous large white cheek patch, white supercilium, and retained the yellow bill flanges. They were easily identifiable up to 7 weeks, even in mixed flocks. We observed the supercilium of juveniles began to turn russet after this period. Juveniles remained with both parents during the first 3 weeks post fledging. We observed them on six occasions after 5 weeks in mono-specific flocks of 4–7 individuals; in one case, two juveniles were with both parents and one unknown adult.

Nest Site.—The seven nests were in the interior (>50 m from the edge) and relatively dense parts of the forest fragments where some boulders with abundant lichens and mosses were also present. The average (± SD) height of trees in which nests were placed was 3.16 ± 0.56 m. The height of nests above ground was 2.43 ± 0.25 m and nests were well camouflaged inside dense foliage.

DISCUSSION

The breeding season of the Giant Conebill extended from October to December, which coincided with the beginning of the rainy season (Nov–Mar) with 10° C mean monthly temperatures (Fernandez et al. 2001). This timing may be related to an increase in the amount of food resources (insects living in *Polylepis* trees) during and especially after the nestling period. This also coincides with records of Giant Conebill fledglings in Puno (Nov) and Cusco (Dec), Peru (Fjeldså and Krabbe 1990). Herzog et al. (2003) similarly observed that most *Polylepis*-inhabiting bird species had peak breeding activity in October and November. However, González and Torres-Mura (2000) report one active nest of the Giant Conebill on 2 March near Belén (Parinacota Province in Chile), which would be at the end of the rainy season.

The shape of the nest (open cup) follows the pattern found in most Thraupidae species for which nests are known (Fjeldså and Krabbe 1990, Isler and Isler 1999). This characteristic of the Giant Conebill is shared with the phylogenetically related species from the *Conirostrum* genus (*C. speciosum*, *C. bicolor*, *C. cinereum*, *C. tamarugense*) (Estades and López-Calleja 1995, Ribon and Simon 1997). However, size and rim thickness (5.5 cm) re-

corded for the nest of Giant Conebill, are much larger than those reported for nests of the Tamarugo Conebill (*Conirostrum tamarugense*) (width 6.5–9 cm, rim 1.5–2 cm) (Estades and Lopez-Calleja 1995) and the Chestnut-vented Conebill (*C. speciosum*) (width 6.2 cm, rim 0.85 cm) (Ribon and Simon 1997).

The large size of the nest of the Giant Conebill is primarily the result of the rim thickness (55% of total width). This could be to assure support and, perhaps more insulation as nest microclimate is important for chick development (Dawson et al. 2005). The densely interwoven mosses in the upper part of the external layer filled the spaces among the twigs and sticks, probably to improve the external structure and increase protection against wind. The presence and thickness of the lining layers of mosses, bark, roots, stems, feathers, and sheep wool in the interior of the nest seemed to additionally insulate the chamber. Temperatures in the high Andes and within *Polylepis* forest can drop drastically at night or after rainfall (from 12° to 1° C; J. R. A. Cahill, pers. obs.). A nest that is well insulated would not be subject to drastic heat loss. The depth of the nest chamber (5 cm) could also protect chicks from heat loss. The depth of this chamber in the nest of the Giant Conebill in *Polylepis rugulosa* is also mentioned by González and Torres-Mura (2000), but no dimensions are given.

Use of *Polylepis* twigs and bark as nesting materials by the Giant Conebill was also reported by González and Torres-Mura (2000) underlining its strong relation with the *Polylepis* habitat and its designation as a *Polylepis* specialist (Fjeldså and Krabbe 1990, Fjeldså and Kessler 1996, Fjeldså 2002). The use of mosses suggests search for a material that is less abundant than that available from *Polylepis*, but which is most probably present in the interior of forest fragments, which are more humid and the canopy is more dense than at edges (Fernández et al. in prep.). Coincidentally, nests were only found in the interior of forest fragments. Apparently, in fragments of *P. besseri*, these areas are selected and more intensively used by Giant Conebills (Cahill and Matthysen 2007).

The Giant Conebill uses mostly plant material for nest construction, which agrees with the phylogenetically related species: Tamarugo Conebill and Chestnut-vented Conebill (Estades and López-Calleja 1995, Ribon and Simon 1997). Use of large amounts of twigs and leaves of a specific tree for the nest of the Giant Conebill is similar to the specific use of the rachis of leaves of Tamarugo (*Prosopis tamarugo*) trees in the nest of the Tamarugo Conebill (Estades and López-Calleja 1995). Moss material in nests of the Giant Conebill has also been recorded for nests of the Moss-backed Tanager (*Bangsia edwardsi*) (Robbins and Glenn 1988) and the Paradise Tanager (*Tangara chilensis*) (Wood et al. 1992).

The nests we found were well camouflaged in *P. besseri* trees. This has also been reported by González and Torres-Mura (2000), who even mention that observations of the parents at the nest were difficult due to the branches and leaves obstructing vision. Nest camouflage could be a strategy to avoid predators that hunt visually. Predation by avian predators, such as the Yungas Pygmy-owl (*Glaucidium bolivianum*), seems to be an imminent risk for the Giant Conebill since it forms and leads flocks (Herzog et al. 2002).

Substrate trees (height 3.16 m) selected by the Giant Conebill were least abundant in three of the four fragments where nests were found. It is possible the largest trees in these fragments, which usually have few branches near the ground, were chosen for terrestrial predator avoidance, although no signs of predation were observed at nests during this study. This apparent selection for tall substrate trees by the Giant Conebill is not found in the phylogenetically related Tamarugo Conebill (Estades and López-Calleja 1995). The clutch size of this species of two coincides with most Thraupidae (Isler and Isler 1987) and with birds at this latitude (Skutch 1985). The nestling period of 14–16 days is similar (within 1–2 days) to the *Tangara* species for which similar data exist (Isler and Isler 1987, Long and Heath 1994).

Human induced fires and logging are the most prevalent threats for *Polylepis* forests at present in the High Andes (Kessler and Driesch 1993, Hensen 2002). Bark, thin twigs, and mosses are likely to be damaged during fires. Pruning also induces open spaces in the canopy and probably a reduction of mosses. Probable nest sites and abundance of nest material could be negatively affected as a con-

sequence. Protection of the habitat of the Giant Conebill is necessary because it is a near threatened species of a monotypic genus.

ACKNOWLEDGMENTS

We thank the people of Sacha Loma and Cuturi for allowing us to work in their forest, and Greissy Arriarán, Claudia Salazar, Lenny Terceros, and Dania Jarro for assistance during field work, and the guidance of Magaly Mercado for plant identification. This study was funded by the Flemish Interuniversity Cooperation (VLIR-IUC), Belgium and the Centro de Biodiversidad y Genética, Universidad Mayor de San Simón, Bolivia.

LITERATURE CITED

BirdLife International. 2006. Species fact sheet: *Oreomanes fraseri*. http://www.birdlife.org (accessed 15 September 2006).

Burns, K. J., S. J. Hackett, and N. K. Klein. 2003. Phylogenetic relationships of neotropical honeycreepers and the evolution of feeding morphology. Journal of Avian Biology 34:360–370.

Cahill, J. R. A. and E. Matthysen. 2007. Habitat use by two specialist birds in High-Andean *Polylepis* forests. Biological Conservation 140:62–69.

Dawson, R. D., C. C. Lawrie, and E. L. O'Brian. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. Oecologia 144:499–507.

Estades, C. F. and M. V. Lopez Calleja. 1995. First nesting record of the Tamarugo Conebill (*Conirostrum tamarugense*). Auk 112:797–800.

Fernandez, M., J. R. A. Cahill, E. Martinez, and J. M. Lazcano. In Prep. Disturbance and edge effects in High-Andean *Polylepis besseri* forests. In prep.

Fernández, M., M. Mercado, S. Arrázola, and E. Martinez. 2001. Estructura y composición florística de un fragmento boscoso de *Polylepis besseri* Hieron subsp. *besseri* en Sacha Loma (Cochabamba). Revista Boliviana de Ecología y Conservación Ambiental 9:15–17.

Fjeldså, J. 2002. Key areas for conserving the avifauna of *Polylepis* forests. Ecotropica 8:125–131.

Fjeldså, J. and M. Kessler. 1996. Conserving the biological diversity of *Polylepis* woodlands of the highlands of Peru and Bolivia—a contribution to sustainable natural resource management. Nordeco, Copenhagen, Denmark.

Fjeldså, J. and N. Krabbe. 1990. Birds of the High Andes. Zoological Museum, University of Copenhagen and Apollo Books, Svendborg, Denmark.

González, G. E. and J. C. Torres-Mura. 2000. Nidificación de *Oreomanes fraseri* (Passeriformes, Fringillidae) en Tarapacá, Andes de Chile. Boletín Chileno de Ornitología 7:19–23.

Greeney, H. F., M. Juiña, and A. F. Sornoza M. 2006. Nest descriptions for *Conothraupis speculigera* and *Thlypopsis ornate* in Ecuador. Boletín SAO Volume 16 (Number 1).

Hansell, M. 2000. Bird nests and construction behavior. Cambridge University Press, Cambridge, United Kingdom.

Hensen, I. 2002. Impacts of anthropogenic activity on the vegetation of *Polylepis* woodlands in the region of Cochabamba, Bolivia. Ecotropica 8:183–204.

Herzog, S. K., R. Soria A., and E. Matthysen. 2003. Seasonal variation in avian community composition in a High-Andean *Polylepis* (Rosaceae) forest fragment. Wilson Bulletin 115:438–445.

Herzog, S. K., R. Soria A., A. Troncoso J., and E. Matthysen. 2002. Composition and structure of avian mixed-species flocks in a High-Andean *Polylepis* forest in Bolivia. Ecotropica 8:133–143.

Isler, M. L. and P. R. Isler. 1987. The tanagers: natural history, distribution, and identification. Smithsonian Institution Press, Washington, D.C., USA.

Isler, M. L. and P. R. Isler. 1999. The tanagers: natural history, distribution, and identification. Smithsonian Institution Press, Washington, D.C., USA.

Kessler, M. 2002. The "*Polylepis* problem": where do we stand? Ecotropica 8:97–110.

Kessler, M. and P. Driesch. 1993. Causas e historia de la destrucción de bosques altoandinos en Bolivia. Ecología en Bolivia 21:1–18.

Long, A. J. and M. F. Heath. 1994. Nesting ecology and helping behavior in the Azure-rumped Tanager in Mexico. Condor 96:1095–1099.

Mazar Barnett, J., G. Pugnali, and M. Della Seta. 1998. Primer registro del Sai grande *Oreomanes fraseri* (Passeriformes: Coerebidae? Thraupidae?) en la Argentina. El Hornero 15:44–46.

Ribon, R. and J. E. Simon. 1997. The nest and eggs of the Chestnut-vented Conebill *Conirostrum speciosum* (Temmick, 1824). Ornitologia Neotropical 8:71–72.

Ridgely, R. S. and G. Tudor. 1989. The birds of South America. Volume I. The oscine passerines. Oxford University Press, Oxford, United Kingdom.

Robbins, M. B. and G. S. Glenn. 1988. First description of the nest and eggs of the Moss-backed Tanager (*Buthraupis* [*Bangsia*] *edwardsi*). Condor 90: 947–948.

Salaberry, M., J. Aguirre, and J. Yañez. 1992. Adiciones a la lista de aves de Chile: descripción de aves nuevas para el país y otros datos ornitológicos. Noticiario Mensual Museo Nacional Historia Natural 321:3–10.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Ornithological Monographs 36:575–594.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. Neotropical birds, ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Vuilleumier, F. 1984. Patchy distribution and systematics of *Oreomanes fraseri* (Aves, Coerebidae) of Andean *Polylepis* woodlands. American Museum Novitates Number 2777:1–17.

Wood, T. M., F. Gallo, and P. K. Donahue. 1992. Observations at a Paradise Tanager nest. Wilson Bulletin 104:360–361.

The Wilson Journal of Ornithology 120(3):550–564, 2008

BIRD DENSITY AND MORTALITY AT WINDOWS

STEPHEN B. HAGER,[1,7] HEIDI TRUDELL,[2,4] KELLY J. MCKAY,[3] STEPHANIE M. CRANDALL,[1,5] AND LANCE MAYER[1,6]

ABSTRACT.—Little is known about impacts to birds from collisions with windows at commercial buildings. We monitored bird mortality from striking windows at five commercial buildings on two college campuses in northwestern and southwestern Illinois. Bird mortality at Augustana College (northwestern), which was evaluated from 2002 to 2006, totaled 215 individuals in 48 species for an average rate of 55 birds/building/year. We calculated a mortality rate of 24 birds/building/year for 2004–2005 from 142 individuals within 37 species at Principia College (southwestern). Mortality of North American migrant (NAM) and neotropical migrant (NTM) birds was higher during migration than during summer or winter. We tested the hypothesis at Augustana that density of birds at a given location will be positively correlated with numbers of birds that die due to strikes with windows. Bird density only partially explained strikes with windows since mortality was also a function of landscaped habitat that attracted birds. Annual bird mortality at commercial buildings may be about five times higher than previous estimates. These buildings may place bird populations at high risk of strikes at windows.
Received 10 May 2007. Accepted 7 September 2007.

Annual bird mortality from collisions with windows in North America could be as high as 1 billion (Klem 1990). Windows may be the most significant cause of mortality second only to habitat loss (Klem 2006). In an evolutionary sense, both the fit and unfit are at risk wherever birds exist in close proximity to windows (Klem 1990).

Experiments and systematic monitoring, mainly at residential structures (e.g., houses), suggest that mortality to birds from collisions with windows is highest in winter (Klem et al. 2004, Klem 2006) or migration and winter (Klem 1989), and disproportionately affects species that frequent bird feeders (Dunn 1993, Klem et al. 2004). It is thought that landscaping features in the vicinity of houses, which maintain bird feeders, provide habitat (shelter and fruiting trees and shrubs) for birds and, thus, increase their vulnerability to window collisions (Klem 1989). It is also known that mortality at skyscrapers in large cities, such as Toronto, Chicago, and New York is significant, but little has been published about the details of negative impacts. Internet reporting by monitoring programs has identified thousands of birds that die annually during spring and fall migration periods; the species most vulnerable are neotropical and North American migrants, and species of conservation concern (New York City Audubon Society 2004, Hunsinger 2005, Fatal Light Awareness Program 2006).

Less attention has been given to studying the impacts to birds at commercial buildings, which may be broadly defined as buildings (~600 m^2) used in service, office, education, and healthcare (Swenson 1997). Recent developments related to commercial building construction may be placing birds at a higher risk of collisions with windows than current estimates of annual bird mortality. We estimated that 5.58 million commercial buildings were in the United States in 2006 which is up 1.63 million since 1986 (Klem 1990, Environmental Protection Agency 2004).

Blem and Willis (1998) suggested that in the last 10–20 years, commercial building construction had increased in suburban areas and these buildings are surrounded by landscaping features that provide food and shelter for birds. We found support for this contention by examining city ordinances which mandate establishment of landscaping around commercial buildings (City of Rock Island, Illinois 2004; City of Wheaton, Illinois 2007). Furthermore, the American So-

[1] Department of Biology, Augustana College, Rock Island, IL 61201, USA.
[2] Principia College, Elsah, IL 62028, USA.
[3] BioEco Research and Monitoring Center, Hampton, IL 61256, USA.
[4] 2218 South 23rd Street, Abilene, TX 79605, USA.
[5] University of Illinois Extension, Rock Island County, 4550 Kennedy Drive, Suite 3, East Moline, IL 61244, USA.
[6] 1006 Oakcrest Street, Apartment 102, Iowa City, IA 52246, USA.
[7] Corresponding author;
e-mail: stevehager@augustana.edu

ciety of Landscape Architects expected that in 2007 the demand would be higher than ever for environmentally-friendly landscaping, which includes adding native plants and water resources in close proximity to commercial buildings (Owens 2006).

One published study detailing the systematic monitoring in suburban Virginia of bird mortality at commercial buildings found: (1) bird mortality was about three times higher than the estimated 1–10 dead birds/building/year, (2) North American and neotropical migrants died at higher proportions compared to permanent residents, and (3) mortality was highest during spring and fall migration and lowest in winter and summer (O'Connell 2001). Similar results were reported by Blem and Willis (1998), whose data came partly from office buildings in Virginia, and by Johnson and Hudson (1976) in an analysis of bird impacts related to a glassed-in walkway connecting two commercial buildings in Washington State.

It is critical that details of mortality due to collisions with windows at commercial buildings be identified given that relatively little is known about the interactions between birds and commercial buildings, and that more of these buildings are being constructed in areas that contain "bird-friendly" habitat. Moreover, little is known about the intrinsic factors affecting whether or not birds fly into windows aside from the contention that birds do not perceive clear and tinted glass as barriers (Klem 1989, Klem et al. 2004). Extrinsic factors thought to affect collision frequency include behavior, window characteristics, and the environment (season, time of day, and weather) (Klem 1989, Klem et al. 2004). In addition, Klem (1989, 2006) hypothesized the best predictor of collision rate at any one site is the density of birds in the vicinity of glass. This hypothesis—hereafter referred to as the bird density hypothesis—was generally supported for bird mortality observed at a house in southern Illinois (Klem 1989) and by Dunn (1993), who analyzed data from Project Feeder Watch (Cornell Laboratory of Ornithology 2006) for the winter months at houses where participants provided estimates of bird abundance only for species observed at feeders.

We present the results of two studies. In Study 1 we systematically monitored avian mortality from strikes at windows at five commercial buildings in northwestern and southwestern Illinois: Augustana College, Rock Island, and Principia College, Elsah, respectively. Our objectives were to: (1) document the abundance and richness of birds killed by buildings, and (2) assess the relationship between season and migratory class of birds killed by windows, and between window area and mortality within sections of a building and among buildings. We tested the bird density hypothesis in Study 2 for a commercial building at Augustana College in spring (Apr–May 2006) and winter (Dec 2006–Jan 2007). Our objective for this study was to evaluate the relationship between estimates of bird density using point counts and birds killed by strikes with windows.

METHODS

Study 1.—We monitored bird mortalities at two geographic locations in Illinois: Augustana College in Rock Island and Principia College in Elsah. Monitoring at Augustana College was conducted at the Science Building (90° 33′ W, 41° 30′ N) from November 2002 to November 2006 (Fig. 1). The college is within the Dissected Hill Plains Physiographic Area (Ruth 2006) and at the edge of a terrace overlooking the Mississippi River (National Cooperative Soil Survey 1998). The slopes of the bluffs are composed of upland hardwood forest, whereas the flat areas are landscaped with a variety of deciduous and evergreen shrubs and trees. The Science Building is at the western edge of campus. The western and southern edges of the building are in close proximity to wooded terrace slopes, while the northern edge faces a parking lot and paved roadway. The eastern side faces the "quad", which is a mosaic of landscaped grasses and woody vegetation including ginkgo (*Ginkgo biloba*), sycamore (*Platanus* spp.), oaks (*Quercus* spp.), maples (*Acer* spp.), and crab apple (*Malus* spp.).

The Science Building is 74 m long, 25 m wide, and four stories in height. The main entry ways (2 along the eastern edge and 1 at the western edge), and the walls in which the entry ways are found, are almost completely glass. Much of the remainder of the eastern and western walls is composed of glass. We identified sections of the building that corre-

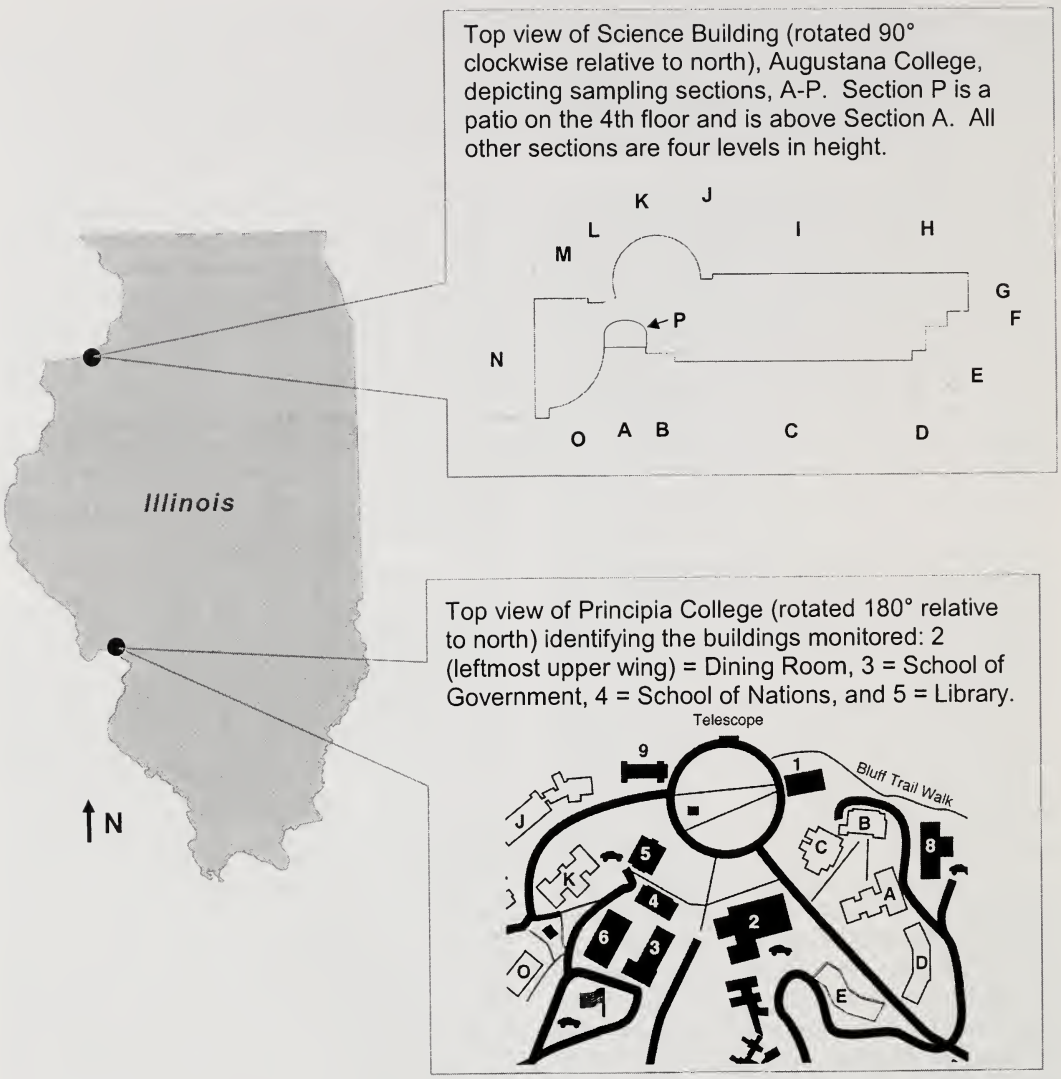


FIG. 1. Locations and building characteristics for studies at Augustana and Principia colleges, Illinois.

sponded to variation in wall characteristics and window size and shape. Each section was given a unique label ranging from "A" through "P" (Fig. 1) and we calculated window area. Little vegetation occurs at the immediate edge of the building and this made visual surveys for dead birds relatively unobstructed. Some ivy ground cover (*Hedera* spp.) occurs at the northeast corner of the building, but the remainder is either paved walkway or decorative stone ground cover.

We monitored avian mortality by completing about two surveys/week around the building. We focused on a 2-m wide transect surrounding the entire building that extended from the building's edge. An analysis of survey effort suggested that two surveys/week, rather than daily surveys, were sufficient to accurately estimate mortality rate. Bodies reported to us by others that were within 2 m of the building were also included in the data set. We assumed that all dead birds adjacent to the building resulted from window collisions.

We salvaged all bodies (including incidental findings exclusive of surveys), identified them to species whenever possible, and placed them in the Vertebrate Museum of Augustana College. Common and scientific names fol-

lowed the American Ornithologists' Union (1998). We also recorded the date and section of the building at which each body was found. Scavengers, grounds workers, custodians, and students may have impacted detection probability. However, we believe that any effect was minimal since many of the faculty, staff, and students at the Science Building were informed of this project and reported bird bodies to us. Moreover, scavengers may have had little impact since some of the bodies found were fairly well decomposed (estimated to be 2–3 days old) and recent work found only 13% of experimental baits were taken or moved slightly from their location by scavengers (Klem et al. 2004).

We tested for differences in average weekly mortality by bird season using Kruskal-Wallis tests. Seasons were defined according to the seasonal movements of passerine birds in the region of northwest and southwest Illinois: (1) North American Migrant (NAM): Fall Migration = 2nd half of September–November, Winter = December–February, Spring Migration = March–1st half of May, Summer Breeding = 2nd half of May–1st half of September; (2) neotropical migrant (NTM): Fall Migration = 2nd half of August–1st half of October, Winter = 2nd half of October–March, Spring Migration = April–May, Summer Breeding = June–1st half of August; and (3) permanent resident (PER): Non-Breeding Season = October–April, Breeding Season = May–September. Differentiating each migratory class in this manner allowed us to more precisely assess the timing of mortality relative to seasonal movements of individuals. We used the log likelihood ratio and examined whether the proportion of birds separated by migratory class was different relative to known proportions (total species = 99; NAM = 45.5%; NTM = 36.4%; PER = 18.1%; S. B. Hager, unpubl. data) at the campus. We conducted simple linear regression to assess the relationship between window area (i.e., building section) and mortality. Normality was examined using the Shapiro Wilk Test (Zar 1984) and all statistical tests were completed using JMP 6 (SAS Institute Inc. 2006).

We monitored bird collisions at Principia College at windows at four commercial buildings (90° 21′ W, 38° 56′ N) between January 2004 and November 2005 (Fig. 1); however, in 2004 we could not monitor from 4 June to 4 September and 20 November to 29 December, nor for July 2005. The college is within the Prairie Peninsula Physiographic Area (Ruth 2006) and is on the bluffs of the Mississippi River (National Cooperative Soil Survey 1999). The general character of campus vegetation is similar in landscaping design and plant species to Augustana.

Standardized surveys for mortality were conducted at the Library, School of Nations, School of Government, and Dining Room (Fig. 1). The Library (Lib) is roughly square in shape and three stories in height. Relatively more vegetation surrounded this building than the others, although this did not impact visual surveys. School of Nations (SN) is two stories in height, roughly rectangular, and contains an irregularly shaped main entrance at the northeast edge of the building. This building was the most difficult at which to conduct surveys due to the presence of creeping vegetation (e.g., *Hedera* spp.) that surrounded most windows. This may have prevented us from retrieving all bodies. School of Government (SG), three stories in height, is "L" shaped from top view. The Dining Room (DR), two stories tall, comprises the eastern section of Howard Center and contains only three sides. No measurements were taken for each building. Qualitatively speaking, we ranked the following for relative size of buildings: SG > Lib > SN > DR; and for window area: Lib > SN > SG > DR.

Survey methods and documentation for salvaging bird bodies followed those used for Augustana, except that daily surveys were completed around each building and all bodies were deposited in the Museum of Natural History, University of California, Santa Cruz. Incidental mortality is reported as the number of bodies opportunistically encountered on campus exclusive of Lib, SN, SG, and DR; these are not included in any statistical analysis.

Kruskal/Wallis Ranked Sums test was used to evaluate differences in mortality for migratory class and bird seasons. We used the log likelihood ratio to examine whether the proportion of birds separated by migratory class was different relative to known proportions (total species = 147; NAM = 36.7%; NTM = 49.0%; PER = 14.3%; M. J. Hoff, unpubl. data) at the campus. Differences in mortality

by building (i.e., estimated window area) were examined using the log likelihood ratio.

Study 2.—We tested the bird density hypothesis at the Augustana College Science Building during spring migration (Apr–May 2006) and winter (Dec 2006–Jan 2007). We chose spring migration since species detection via singing males, including non-breeding migrants, could be maximized relative to fall, when male singing is rare for most species. A winter analysis was used so that comparisons could be made with spring since other studies speculated that window-caused mortality is low in winter as fewer birds may be present at a site (Johnson and Hudson 1976, Klem 1989, Blem and Willis 1998).

We assessed avian richness and abundance in spring with fixed radius (50 m) point counts, which were 10 min in duration (Bibby et al. 2000). The Science Building is disproportionately long along a north-south axis and we established one point count station each on the west facing (Augie Point #1) and east facing (Augie Point #2) sides of the building. One point count survey was completed on Saturdays of each week between 0700–0800 hrs CDT (surveys on 28 Apr and 5 May were completed on Friday). Data from both point count stations were combined for each survey date. We followed the weather protocol for the North American Breeding Bird Survey (Pardieck 2001). Weekly point count data were compared to the number of dead birds discovered 3 days prior to and 3 days following the point count (surveys completed on a Friday were compared to mortality 2 days prior and 4 days after this day). We assumed for this comparison that (1) migration for a species at a specific location may be several weeks in duration (Devore et al. 2004), and (2) within individuals, average stopover times would be ~1 week in duration given data for White-crowned Sparrow (*Zonotrichia leucophrys*) and Wood Thrush (*Hylocichla mustelina*) (Chilton et al. 1995, Wang and Moore 1997), and recent mathematical models (Schaub et al. 2001, Efford 2005).

We used the same point count survey methodology for winter as in spring to estimate species abundance and richness except that surveys were completed between 0700 and 0800 hrs CST. We believe these methods were appropriate for winter since bird populations are generally stable during this season, as was found for winter home ranges in the Northern Cardinal (*Cardinalis cardinalis*) (Halkin and Linville 1999).

Bird mortality due to collisions with windows reported by others was highest in the spring and fall at commercial buildings (Johnson and Hudson 1976, Blem and Willis 1998, O'Connell 2001). Thus, based on the bird density hypothesis, we predicted the following at the Science Building: (1) in spring, a time of high mortality, bird abundance would be relatively high; (2) in winter, a time of low mortality, bird abundance would be relatively low; and (3) the abundance and richness of species killed at windows will be proportional to the abundance and richness of birds living in the vicinity of the building.

We used simple linear regression to analyze the relationship between the abundance of mortalities and living birds, as well as the richness of mortalities and living birds within season. The Kruskal-Wallis Ranked Sums test was used to evaluate the abundance of mortalities to the abundance of living birds for each species. Differences in abundance and richness of living birds for spring and winter were assessed using ANOVA.

RESULTS

Study 1.—We documented 215 window-killed birds within 48 species at Augustana College (Fig. 2, Appendix 1). Average mortality was 54.8 birds/building/year. Species with ≥10 dead individuals (this level appeared to be a natural break in the data) included White-throated Sparrow (*Zonotrichia albicollis*), Ovenbird (*Seiurus aurocapilla*), American Robin (*Turdus migratorius*), Swainson's Thrush (*Catharus ustulatus*), Dark-eyed Junco (*Junco hyemalis*), Ruby-throated Hummingbird (*Archilochus colubris*), and Northern Cardinal. These represented 44.2% of the total mortality at the Science Building. Nine to 12 new species were added each year after an initial species total of 23 in 2003 (including 8 weeks in 2002).

The mean weekly rate of mortality for each migratory class (Fig. 3) differed among bird-defined seasons (NAM: $H = 35.9$, $P < 0.0001$; NTM: $H = 72.9$, $P < 0.0001$; PER: $H = 6.33$, $P = 0.012$). The proportions of window-killed NAMs (39.9%), NTMs (54.2%)

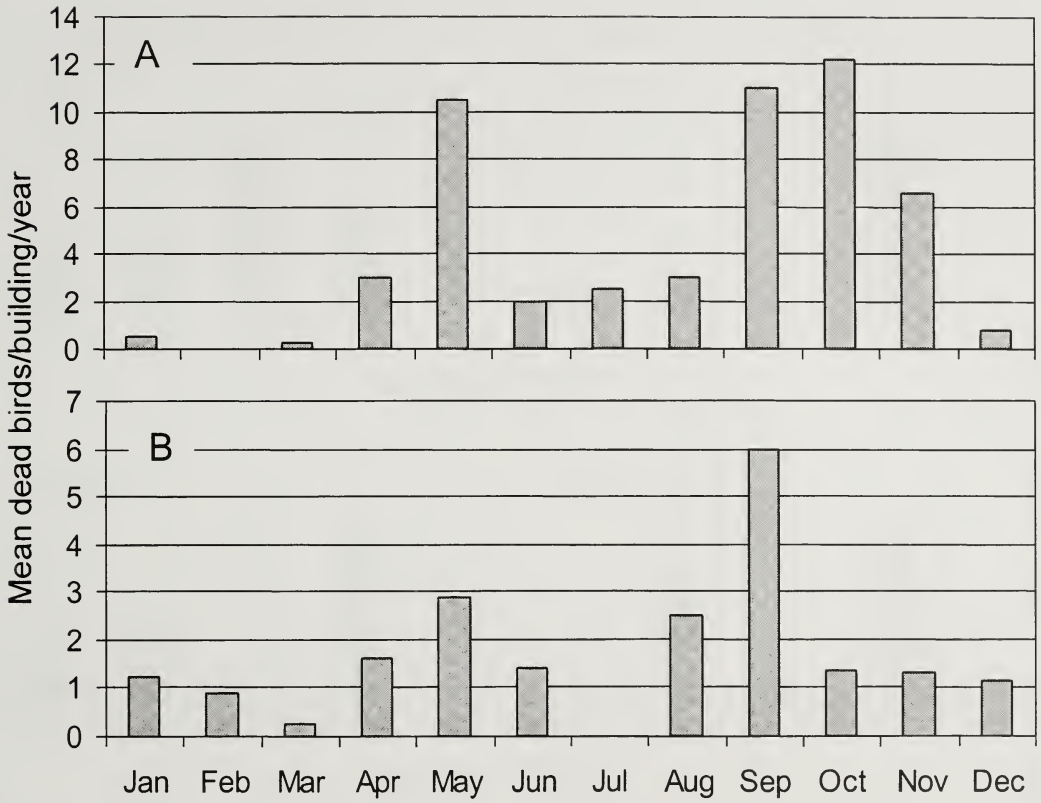


FIG. 2. Detections of dead birds/building/year, (A) 2002–2006 at Augustana College and (B) 2004–2005 at Principia College, Illinois.

and PERs (6.3%) differed from proportions known to occur on campus ($G = 9.06$, df = 2, $P = 0.011$). There was a significant positive relationship between window area and mortality for each building section ($n = 16$, $r^2 = 0.54$, $P = 0.0012$).

We documented 142 window-killed individuals of 37 species at Principia College (Fig. 2, Appendix 1). Average mortality was 24.0 birds/building/year. Species killed most often (≥8 individuals; natural break in the data) included Ruby-throated Hummingbird, American Robin, White-throated Sparrow, and Ovenbird. These species represented 56.3% of the total mortality. Twelve new species were found in 2005 relative to those found in 2004. Incidental mortality totaled 58 individuals, which were dominated by the same species recorded during standardized surveys, except for Ovenbirds (Appendix 1).

The mean weekly rate of mortality (Fig. 3) differed among seasons for NTMs ($H = 34.3$, $P < 0.0001$), but not for NAMs ($H = 3.24$, $P = 0.36$) or PERs ($H = 0.69$, $P = 0.41$). The proportions of window-killed NAMs (29.7%), NTMs (54.1%), and PERs (16.2%) was not different from proportions known to occur on campus ($G = 0.81$, df = 2, $P = 0.67$). Significantly more birds died from collisions with windows at Lib (71.1%) than at SG (11.3%), SN (11.3%), and DR (6.30%) ($G = 135.5$, df = 3, $P < 0.0001$); this corresponded to qualitative estimates of window area by building. This may also be explained by the finding that all dead Ruby-throated Hummingbirds, which had the highest mortality at Principia, were at Lib; however, significantly more birds died at Lib than at the other buildings ($G = 56.1$, df = 3, $P < 0.0001$) even if hummingbirds are excluded from the data set.

Study 2.—We documented 55 and 22 live species during spring and winter, respectively (Table 1, Appendix 2). Simple linear regression revealed no relationship between dead

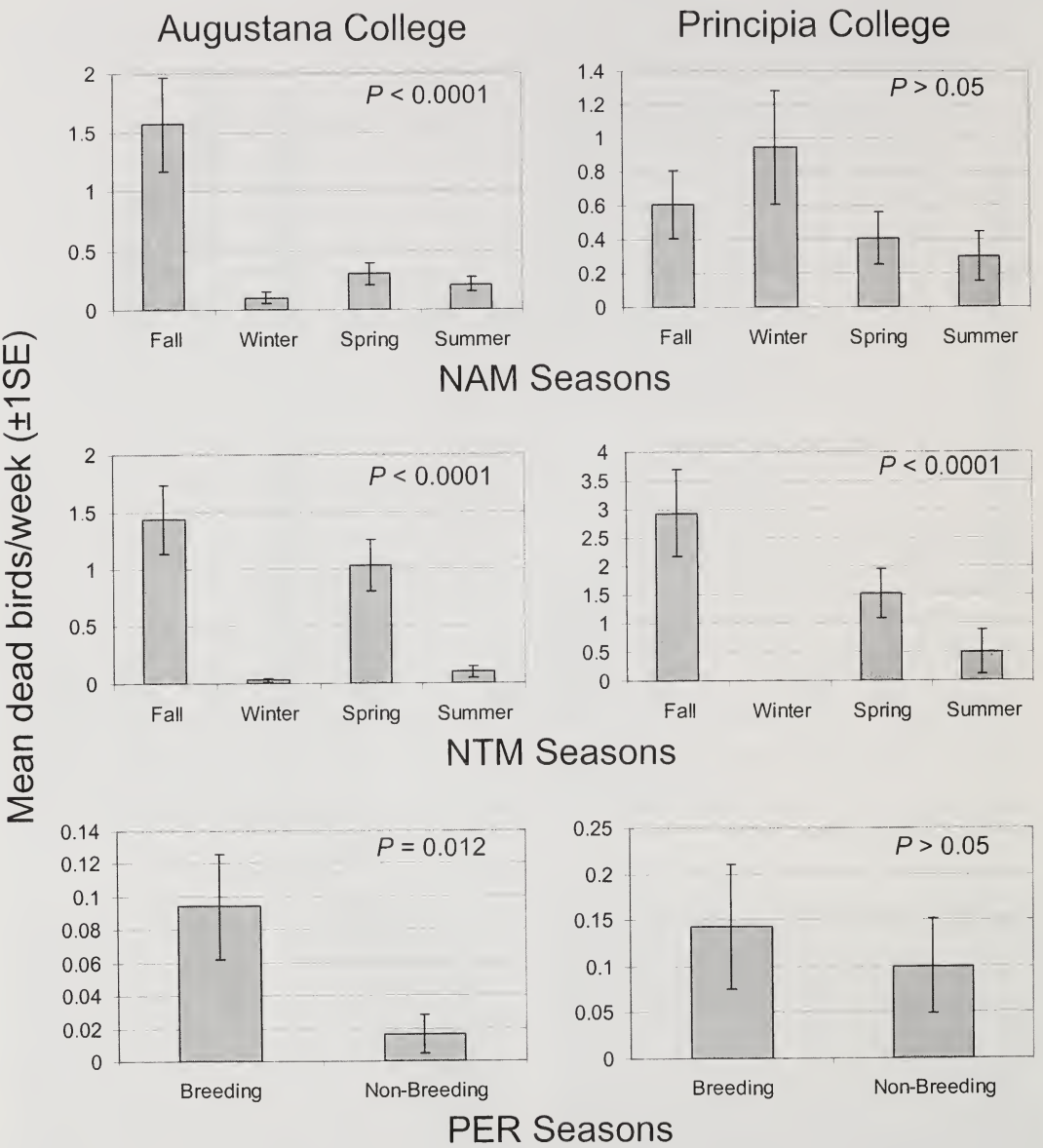


FIG. 3. Detections of dead birds/week for bird-defined seasons separated by campus and migratory class, Augustana and Principia colleges, Illinois.

and living birds for abundance ($n = 8$, $r^2 = 0.014$, $P = 0.79$) and richness ($n = 8$, $r^2 = 0.18$, $P = 0.29$) in spring. We found no relationship in spring between species of living birds observed around the Science Building and those that were killed, all surveys combined ($H = 23.1$, $P = 0.57$). In spring, only 8 of 55 (14.5%) species observed during point count surveys were recorded as window-killed. We found no window-killed birds in winter despite relatively abundant species (defined as >5 individuals/survey), such as American Crow (*Corvus brachyrhynchos*), American Robin, European Starling (*Sturnus vulgaris*), Cedar Waxwing (*Bombycilla cedrorum*), Dark-eyed Junco, Northern Cardinal, and House Sparrow (*Passer domesticus*). We found no differences in the abundances of living birds between spring and winter ($F = 2.81$, $P = 0.12$); however, richness in living

TABLE 1. Abundance of birds at point counts and birds found dead near windows at Augustana College, Illinois in Study 2.

Season Observation date[a]	# Live birds		# Birds found dead	
	Abundance	Richness	Abundance	Richness
Spring				
8 Apr 2006	113	25	2	1
15 Apr 2006	98	25	0	0
22 Apr 2006	101	20	0	0
28 Apr 2006	107	17	1	1
5 May 2006	70	22	4	3
13 May 2006	76	22	1	1
20 May 2006	127	32	3	3
27 May 2006	85	22	2	2
Mean ± SE	97.1 ± 6.80	23.13 ± 1.56	1.63 ± 0.50	1.38 ± 0.42
Winter				
6 Dec 2006	128	16	0	0
12 Dec 2006	86	14	0	0
20 Dec 2006	87	12	0	0
27 Dec 2006	68	14	0	0
3 Jan 2007	68	16	0	0
10 Jan 2007	71	13	0	0
19 Jan 2007	73	14	0	0
25 Jan 2007	59	10	0	0
Mean ± SE	80.0 ± 7.62	13.6 ± 0.71		

[a] Weekly point count data were compared to bird kills discovered ± 3 days relative to the date on which a point count survey was conducted.

birds differed between these seasons (F = 30.7, $P < 0.0001$). Relatively abundant species observed during point counts in both spring and winter experienced no mortality from window collisions, including American Robin, Northern Cardinal, and House Sparrow. The monitoring data revealed no differences among years for mortality in spring (H = 1.81, P = 0.61) and winter (H = 4.59, P = 0.33). Thus, the mortality we documented in spring 2006 and winter 2006–2007 was not different than the mortality observed for these same seasons in previous years.

DISCUSSION

The results of systematic monitoring of window strikes at commercial buildings in northwestern and southwestern Illinois (Study 1) demonstrate that bird mortality was high. We calculated a mortality rate of almost 55 dead birds/building/year at Augustana (northwestern Illinois); this is about twice as high as Principia in southwestern Illinois (24 birds/building/year) and relative to an office park (29 birds/building/year) in Richmond, Virginia (O'Connell 2001). Bird mortality was highest among sections of the Science Building with the most window area and corresponded to buildings at Principia with the highest estimated window area. Species richness of bird mortality was higher at Augustana (n = 48) than at Principia (n = 37) and in Virginia (n = 40; O'Connell 2001). Differences among sites in numbers and species of birds dying may be a consequence of factors related to behavior, environment, and window area. We found that 9 to 12 new species died each year at both Augustana and Principia. Thus, multiyear studies may observe a larger range of species dying from collisions with windows than monitoring projects of relatively short duration (O'Connell 2001).

Mortality for Study 1 at Augustana and Principia was high for particular species: Ruby-throated Hummingbird, American Robin, White-throated Sparrow, and Ovenbird. Swainson's Thrush, Northern Cardinal, and Dark-eyed Junco also died at high rates at Augustana. Deaths of Ruby-throated Hummingbirds at Principia were more than twice as high as other species; about half of these deaths occurred in September, which includes the peak of fall migration in this region (Robinson et al. 1996). Robinson et al. (1996) iden-

tified Ruby-throated Hummingbirds as being possibly vulnerable to window strikes and Graham (1997) suggested that traplining (foraging for nectar over great distances of undefended plants) of hummingbirds may make them vulnerable to collisions. High abundance of this species in southwestern Illinois (K. J. McKay, pers. obs.) coupled with fall flowering honeysuckle (*Lonicera* spp.) on the Principia campus (M. J. Hoff, pers. obs.) may attract high numbers during fall migration. White-throated Sparrows at Augustana were killed more often than other species. Most individuals (72%) died in the fall, a time during which migration for this sparrow is more prolonged than during spring (Borror 1948). We found individuals from September through November, whereas spring mortality was restricted to May.

Our work contributes toward a better understanding of those species commonly killed at windows of different building structures. Regular fatalities at commercial buildings include Ruby-throated Hummingbird, Yellow-bellied Sapsucker (*Sphyrapicus varius*), Brown Creeper (*Certhia americana*), thrushes, waxwings, and wood-warblers (Klem 1989, Blem and Willis 1998, O'Connell 2001), whereas at houses they are grosbeaks, chickadees, and woodpeckers (Klem 1989, Dunn 1993). Some species are common at both structures: kinglets, American Robin, Northern Cardinal, White-throated Sparrow, Dark-eyed Junco, finches, and House Sparrow (Klem 1989, Dunn 1993, Blem and Willis 1998, O'Connell 2001).

To our knowledge, this is the first study to examine mortality of migratory classes against proportions known from a site and across specific bird-defined seasons for each migratory class. These analyses allowed us to more precisely understand bird mortality related to seasons. Generally, migrating species tended to die relatively more during spring and fall migration, although patterns of seasonal mortality were different between campuses. We believe the lack of monitoring surveys conducted in summer and December at Principia resulting in less than a full year of monitoring data, explains part of these differences. In addition, differences may be attributed to variation in the composition of bird populations among seasons at each site.

We tested the bird density hypothesis in Study 2 at the Science Building of Augustana. We predicted the following at this building: (1) in spring, a time of high mortality, bird abundance would be relatively high, (2) in winter, a time of low mortality, bird abundance would be relatively low, and (3) the abundance and richness of species killed at windows will be proportional to the abundance and richness of birds living in the vicinity of the building. Only the first of these predictions was supported by the data. Thus, our work does not support the bird density hypothesis *per se*. Our data suggest that in addition to bird density, window-related factors and bird behavior (Klem 1989) explain the patterns of collisions at windows observed at the Science Building. The hypothesis of window-related factors indicates that habitat variables attract particular avian species to the vicinity of windows which results in these species being more vulnerable to dying at windows than birds not found near windows. Factors in this explanation include: size and location of windows in a building relative to ground level; suburban and urban habitats; and habitat surrounding buildings that contains bird feeding stations, fruiting trees, water supplies, and nesting and perching sites (Klem 1989). The bird behavior hypothesis suggests that collisions with windows occur due to intra- and interspecific interactions (e.g., male-male chasing and escape flights due to sudden presence of a potential predator) and physiological effects to the body during migration, e.g., migratory restlessness and aggression (Klem 1989, Berthold 2001).

The results of Study 2 are consistent with these hypotheses because: (1) mortality was documented in spring and not in winter despite the observation during point counts of no significant differences in abundance between these two time periods; (2) there was no relationship for species richness between birds found living near the building and those that died; (3) for birds that did not die from collisions with windows, abundances were similar between spring and winter (e.g., Mourning Dove [*Zenaida macroura*], Downy Woodpecker [*Picoides pubescens*], and House Finch [*Carpodacus mexicanus*]) or the species was more abundant in one season or another (e.g., American Crow and Cedar Waxwing); (4) abundance was higher in

winter for some birds that died in spring (e.g., European Starling); and (5) relatively abundant birds did not die at windows during Study 2 (e.g., Northern Cardinal and House Sparrow) (Table 1, Appendix 2). Only one season each for spring and winter was examined for this work, but the mortality data were not statistically different among years for these seasons; several bird surveys completed on the Augustana campus in previous years in winter and spring suggest that abundance and diversity were similar among years (S. B. Hager, unpubl. data).

The bird density hypothesis was previously supported for houses during winter, and landscaping features and bird behavior (related to anti-predation) were found to contribute to collisions at windows (Dunn 1993). Our results for a commercial building suggest that birds are vulnerable to collisions with windows for different reasons. The presence of bird feeding stations at houses may best explain these differences. Dunn (1993) noted that houses maintaining feeders attracted a minimum of 84 birds during a count period, which tends to confine high densities to a relatively small area near a house. Mortality at houses is known to occur from the sudden presence of a potential predator that forced birds to abruptly take flight, but fail to recognize windows of a house as a barrier (Dunn 1993). Klem et al. (2004) found a significant positive relationship between increasing distance of feeders from houses and the rate of bird-window collisions. Thus, it seems that window strikes by birds occur when densities per unit area are high and birds are congregated some distance from the structure. We observed similar abundances at the Science Building as those reported by Dunn (1993) and suggest the density of birds was relatively lower when compared to the area available to birds at a house. In addition, birds known to frequent feeders in winter, such as Dark-eyed Junco, Northern Cardinal, and House Sparrow, were common at the Science Building, but experienced no mortality during Study 2. Houses with feeder stations may increase bird density beyond some threshold value that significantly increases their vulnerability to windows strikes. Conversely, at commercial buildings without feeding stations, bird density per unit area and vulnerability to colliding with windows are relatively low.

We suggest that birds in the United States and Canada are vulnerable to window collisions because: (1) increasing numbers of commercial buildings each year, zoning laws for and societal interest in increased naturalized habitat around houses and businesses, and that each of these is more common in suburban contexts (Blem and Willis 1998; Owens 2006; C. G. Mahaffey, pers. comm.); (2) bird mortality due to window collisions at commercial buildings disproportionately affects neotropical and North American migrants mostly during spring and fall migration; and (3) the reported annual mortality at commercial buildings is at least 3–5 times higher than estimated by Klem (1990). We recommend implementing measures directed at disrupting factors which place birds at high risk of striking windows. The most practical in the context of heightened interest by the public in naturalized landscaping are external window screening that covers windows and angled window mounting in buildings (Klem 2006). These significantly reduce mortality by migratory and non-migratory species (Klem et al. 2004, Klem 2006). Proper placement of bird feeders, if present in the vicinity of a building, appears to be effective in reducing mortality to species that frequent feeding stations (Klem et al. 2004).

ACKNOWLEDGMENTS

All window-killed birds at Augustana College were salvaged under Federal Migratory Bird Scientific Collecting Permit MB096406-0 and Illinois DNR Scientific Collecting Permit NH07.313. We are grateful to S. A. Hallstrom, who helped with monitoring bird mortality throughout the study at Augustana. A. B. Francois assisted in fall 2005. M. J. Hoff kindly provided a species list for Principia College. J. J. Williams offered insightful comments on an early draft of the paper. We thank Daniel Klem Jr. and one anonymous reviewer for helpful suggestions on the manuscript.

LITERATURE CITED

American Ornithologists' Union. 1998. Check-list of North American birds. Seventh Edition. American Ornithologists' Union, Washington, D.C., USA.

Berthold, P. 2001. Bird migration: a general survey. Second Edition. Oxford University Press, New York, USA.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. Mustoe. 2000. Bird census techniques. Second Edition. Academic Press, London, United Kingdom.

Blem, C. R. and B. A. Willis. 1998. Seasonal variation of human-caused mortality of birds in the Richmond area. The Raven 69:3–8.

Borror, D. J. 1948. Analysis of repeat records of banded White-throated Sparrows. Ecological Monographs 18:411–430.

Chilton, G., M. C. Baker, C. D. Barrentine, and M. A. Cunningham. 1995. White-crowned Sparrow (*Zonotrichia leucophrys*). The birds of North America. Number 183.

City of Rock Island, Illinois. 2004. Rock Island Illinois Zoning Ordinance. www2.rigov.org/pdf/ordinances/zoningordinance.pdf (accessed 16 January 2007).

City of Wheaton, Illinois. 2007. Wheaton Zoning Ordinance. www.wheaton.il.us/Service/Planning-D/index.htm (accessed 27 January 2007).

Cornell Laboratory of Ornithology. 2006. Project feeder watch. Cornell Laboratory of Ornithology, Ithaca, New York, USA. www.birds.cornell.edu/pfw (accessed 2 January 2007).

Devore, S., S. D. Bailey, and G. Kennedy. 2004. Birds of Illinois. Lone Pine Publishing, Edmonton, Alberta, Canada.

Dunn, E. H. 1993. Bird mortality from striking residential windows in winter. Journal of Field Ornithology 64:302–309.

Efford, M. G. 2005. Migrating birds stop over longer than usually thought: comment. Ecology 86:3415–3418.

Environmental Protection Agency. 2004. Buildings and the environment: a statistical summary compiled by: U.S. Environmental Protection Agency Green Building Workgroup. Washington, D.C., USA. www.epa.gov/greenbuilding/pubs/gbstats.pdf (accessed 20 January 2007).

Fatal Light Awareness Program. 2006. Collision data. www.flap.org/new/nestegg_3.htm. Fatal Light Awareness Program, Toronto, Ontario, Canada (accessed 3 January 2007).

Graham, D. L. 1997. Spider webs and windows as potentially important sources of hummingbird mortality. Journal of Field Ornithology 68:98–101.

Halkin, S. L. and S. U. Linville. 1999. Northern Cardinal (*Cardinalis cardinalis*). The birds of North America. Number 440.

Hunsinger, R. L. 2005. Chicago bird collision monitors: prospects for a Great Lakes network. Passenger Pigeon 67:113–116.

Johnson, R. E. and G. E. Hudson. 1976. Bird mortality at a glassed-in walkway in Washington State. Western Birds 7:99–107.

Klem Jr., D. 1989. Bird-window collisions. Wilson Bulletin 101:606–620.

Klem Jr., D. 1990. Collisions between birds and windows: mortality and prevention. Journal of Field Ornithology 61:120–128.

Klem Jr., D. 2006. Glass: a deadly conservation issue for birds. Bird Observer 34:73–81.

Klem Jr., D., D. C. Keck, K. L. Marty, A. J. Miller Ball, E. E. Niciu, and C. T. Platt. 2004. Effects of window angling, feeder placement, and scavengers on avian mortality at plate glass. Wilson Bulletin 116:69–73.

National Cooperative Soil Survey. 1998. Soil survey of Rock Island County, Illinois. USDA, Natural Resources Conservation Service, Washington, D.C., USA. soildatamart.nrcs.usda.gov/Manuscripts/IL161/0/RockIsland_IL.pdf (accessed 12 January 2007).

National Cooperative Soil Survey. 1999. Soil survey of Madison County, Illinois. USDA, Natural Resources Conservation Service, Washington, D.C., USA. soildatamart.nrcs.usda.gov/Manuscripts/IL119/0/madison_IL.pdf (accessed 14 January 2007).

New York City Audubon Society. 2004. List of birds found dead and injured at selected buildings in New York City, 1990 to spring 2001. New York City Audubon Society, New York, USA. www.birdbash.org/NYCASBirdWatch/BirdKillsCumulativebyStatusonly.htm (accessed 29 March 2004).

O'Connell, T. J. 2001. Avian window strike mortality at a suburban office park. The Raven 72:141–149.

Owens, A. 2006. Landscape architects identify trends for 2007. American Society of Landscape Architects, Washington, D.C., USA. www.asla.org/press/2006/release122106.htm (accessed 27 January 2007).

Pardieck, K. 2001. North American Breeding Bird Survey. Training: main menu. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.pwrc.usgs.gov/bbs/participate/training (accessed 15 January 2007).

Robinson, T. R., R. R. Sargent, and M. B. Sargent. 1996. Ruby-throated Hummingbird (*Archilochus colubris*). The birds of North America. Number 204.

Ruth, J. M. 2006. Partners in Flight, Physiographic Area Map. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.partnersinflight.org (accessed 14 January 2007).

SAS Institute. 2006. JMP 6. SAS Institute Inc., Cary, North Carolina, USA.

Schaub, M., R. Pradel, L. Jenni, and J.-D. Lebreton. 2001. Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. Ecology 82:852–859.

Swenson, A. 1997. Profile of commercial buildings in 1995. Energy Information Administration, Washington, D.C., USA. www.eia.doe.gov/emeu/cbecs/char95/profile.html (accessed 20 January 2007).

Wang, Y. and F. R. Moore. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114: 263–278.

Zar, J. H. 1984. Biostatistical analysis. Second Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

APPENDIX 1. Species of window-killed birds (n = 69) documented for Study 1 at both campuses, including Principia incidentals (n = 22), which were opportunistically collected on the Principia campus exclusive of the locations of standardized building surveys.

Common name	Scientific name	Migration status	Augustana College	Principia College	Principia incidentals	Totals
Sharp-shinned Hawk	*Accipiter striatus*	NAM			1	1
Mourning Dove	*Zenaida macroura*	NAM	4	3	2	9
Yellow-billed Cuckoo	*Coccyzus americanus*	NTM			1	1
Chimney Swift	*Chaetura pelagica*	NTM		1		1
Ruby-throated Hummingbird	*Archilochus colubris*	NTM	11	41	10	62
Yellow-bellied Sapsucker	*Sphyrapicus varius*	NAM	8	2		10
Downy Woodpecker	*Picoides pubescens*	PER		1		1
Northern Flicker	*Colaptes auratus*	NAM		1		1
Empidonax flycatcher	*Empidonax* spp.	NTM	1			1
Eastern Phoebe	*Sayornis phoebe*	NAM	1			1
Red-eyed Vireo	*Vireo olivaceus*	NTM	1	1		2
American Crow	*Corvus brachyrhynchos*	PER		1		1
Black-capped Chickadee	*Poecile atricapillus*	PER		1		1
Tufted Titmouse	*Baeolophus bicolor*	PER		1	1	2
White-breasted Nuthatch	*Sitta carolinensis*	PER	2			2
Brown Creeper	*Certhia americana*	NAM	4			4
Carolina Wren	*Thryothorus ludovicianus*	PER			1	1
House Wren	*Troglodytes aedon*	NTM	1			1
Marsh Wren	*Cistothorus palustris*	NAM	1			1
Golden-crowned Kinglet	*Regulus satrapa*	NAM	1	2		3
Blue-gray Gnatcatcher	*Polioptila caerulea*	NTM			1	1
Veery	*Catharus fuscescens*	NTM	1			1
Gray-cheeked Thrush	*C. minimus*	NTM	1	1		2
Swainson's Thrush	*C. ustulatus*	NTM	13	3		16
Hermit Thrush	*C. guttatus*	NAM	5			5
Wood Thrush	*Hylocichla mustelina*	NTM		7		7
American Robin	*Turdus migratorius*	NAM	14	18	3	35
Gray Catbird	*Dumetella carolinensis*	NTM	4			4
Brown Thrasher	*Toxostoma rufum*	NAM	1			1
European Starling	*Sturnus vulgaris*	PER	1			1
Cedar Waxwing	*Bombycilla cedrorum*	NAM	9	4	1	14
Tennessee Warbler	*Vermivora peregrina*	NTM	6	5	1	12
Orange-crowned Warbler	*V. celata*	NTM	1			1
Nashville Warbler	*V. ruficapilla*	NTM	7			7
Yellow Warbler	*Dendroica petechia*	NTM	1			1
Chestnut-sided Warbler	*D. pensylvanica*	NTM	1			1

APPENDIX 1. Continued.

Common name	Scientific name	Migration status	Augustana College	Principia College	Principia incidentals	Totals
Magnolia Warbler	*D. magnolia*	NTM	2	1		3
Cape May Warbler	*D. tigrina*	NTM		1		1
Yellow-rumped Warbler	*D. coronata*	NAM	1		2	3
Black-throated Green Warbler	*D. virens*	NTM		1		1
Yellow-throated Warbler	*D. dominica*	NTM		1		1
Black-and-white Warbler	*Mniotilta varia*	NTM	3	1		4
American Redstart	*Setophaga ruticilla*	NTM	2			2
Ovenbird	*Seiurus aurocapilla*	NTM	16	8	1	25
Northern Waterthrush	*S. noveboracensis*	NTM		1		1
Louisiana Waterthrush	*S. motacilla*	NTM		1		1
Kentucky Warbler	*Oporornis formosus*	NTM	1	1	1	3
Connecticut Warbler	*O. agilis*	NTM	1			1
Mourning Warbler	*O. philadelphia*	NTM	2			2
Common Yellowthroat	*Geothlypis trichas*	NTM	3			3
Canada Warbler	*Wilsonia canadensis*	NTM	2	1	1	4
Summer Tanager	*Piranga rubra*	NTM		2		2
American Tree Sparrow	*Spizella arborea*	NAM		1		1
Chipping Sparrow	*S. passerina*	NTM	1	1	2	4
Fox Sparrow	*Passerella iliaca*	NAM	3			3
Song Sparrow	*Melospiza melodia*	NAM	3			3
Lincoln's Sparrow	*M. lincolnii*	NTM	1			1
Swamp Sparrow	*M. georgiana*	NAM	4			4
White-throated Sparrow	*Zonotrichia albicollis*	NAM	25	13	8	46
Dark-eyed Junco	*Junco hyemalis*	NAM	12	3	4	19
Northern Cardinal	*Cardinalis cardinalis*	PER	10	5	5	20
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	NTM	5			5
Indigo Bunting	*Passerina cyanea*	NTM	4	1	1	6
Common Grackle	*Quiscalus quiscula*	NAM	1	1		2
Brown-headed Cowbird	*Molothrus ater*	NAM	1			1
House Finch	*Carpodacus mexicanus*	PER			2	2
Pine Siskin	*Carduelis pinus*	NAM		2		2
American Goldfinch	*C. tristis*	NAM	4	3	2	9
House Sparrow	*Passer domesticus*	PER			7	7
Unidentified species			8			8
Totals			215	142	58	415

APPENDIX 2. Species observed in Study 2 at Augustana College during point count surveys (n = 16) and monitoring surveys for window-killed birds. No dead birds were found in winter 2006–7.

			Spring 2006		Winter 2006–7
Common name	Scientific name	Migration status	# live/ survey	# dead[a]	# live/ survey
Canada Goose	*Branta canadensis*	NAM	0.3		
Wood Duck	*Aix sponsa*	NAM	0.3		
Mallard	*Anas platyrhynchos*	NAM			0.4
Bald Eagle	*Haliaeetus leucocephalus*	NAM			0.1
Sharp-shinned Hawk	*Accipiter striatus*	NAM	0.1		
Ring-billed Gull	*Larus delawarensis*	NAM			0.1
Rock Pigeon	*Columba livia*	PER	1.4		1.1
Mourning Dove	*Zenaida macroura*	NAM	2.5		2.9
Chimney Swift	*Chaetura pelagica*	NTM	2.6		
Ruby-throated Hummingbird	*Archilochus colubris*	NTM	0.3		
Red-bellied Woodpecker	*Melanerpes carolinus*	PER	0.1		0.1
Yellow-bellied Sapsucker	*Sphyrapicus varius*	NAM	0.6	2	
Downy Woodpecker	*Picoides pubescens*	PER	1.0		1.1
Northern Flicker	*Colaptes auratus*	NAM	0.8		
Eastern Wood-Pewee	*Contopus virens*	NTM	0.3		
Yellow-bellied Flycatcher	*Empidonax flaviventris*	NTM	0.1		
Least Flycatcher	*E. minimus*	NTM	0.4		
Blue-headed Vireo	*Vireo solitarius*	NTM	0.1		
Warbling Vireo	*V. gilvus*	NTM	0.1		
Red-eyed Vireo	*V. olivaceus*	NTM	0.3		
Blue Jay	*Cyanocitta cristata*	PER	4.8		0.4
American Crow	*Corvus brachyrhynchos*	PER	0.9		5.4
Black-capped Chickadee	*Poecile atricapillus*	PER	2.3		1.5
Tufted Titmouse	*Baeolophus bicolor*	PER	0.5		
White-breasted Nuthatch	*Sitta carolinensis*	PER	0.4		0.8
Brown Creeper	*Certhia americana*	NAM	0.1		
Carolina Wren	*Thryothorus ludovicianus*	PER	0.3		
House Wren	*Troglodytes aedon*	NTM	1.1		
Golden-crowned Kinglet	*Regulus satrapa*	NAM	0.6		
Ruby-crowned Kinglet	*R. calendula*	NAM	2.5		
Veery	*Catharus fuscescens*	NTM	0.1		
Gray-cheeked Thrush	*C. minimus*	NTM	0.3		
Swainson's Thrush	*C. ustulatus*	NTM	1.0	2	
Hermit Thrush	*C. guttatus*	NAM	0.9		
Wood Thrush	*Hylocichla mustelina*	NTM	0.1		
American Robin	*Turdus migratorius*	NAM	6.8		6.5
Gray Catbird	*Dumetella carolinensis*	NTM	0.3		
European Starling	*Sturnus vulgaris*	PER	5.4	1	8.8
Cedar Waxwing	*Bombycilla cedrorum*	NAM	2.9		8.4
Tennessee Warbler	*Vermivora peregrina*	NTM	0.9		
Nashville Warbler	*V. ruficapilla*	NTM	0.1		
Northern Parula	*Parula americana*	NTM	0.1		
Yellow Warbler	*Dendroica petechia*	NTM	0.1		
Yellow-rumped Warbler	*D. coronata*	NAM	1.0		
American Redstart	*Setophaga ruticilla*	NTM	0.5		
Ovenbird	*Seiurus aurocapilla*	NTM	0.4	2	
Chipping Sparrow	*Spizella passerina*	NTM	6.1	1	
Fox Sparrow	*Passerella iliaca*	NAM	0.1		
Song Sparrow	*Melospiza melodia*	NAM	0.1		
White-throated Sparrow	*Zonotrichia albicollis*	NAM	0.8	1	0.4
Dark-eyed Junco	*Junco hyemalis*	NAM	0.6		10.4
Northern Cardinal	*Cardinalis cardinalis*	PER	12.3		6.4
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	NTM	0.8	2	
Indigo Bunting	*Passerina cyanea*	NTM	0.4	2	

APPENDIX 2. Continued.

Common name	Scientific name	Migration status	Spring 2006 # live/ survey	Spring 2006 # dead[a]	Winter 2006–7 # live/ survey
Red-winged Blackbird	*Agelaius phoeniceus*	NAM	1.3		
Common Grackle	*Quiscalus quiscula*	NAM	2.4		
Brown-headed Cowbird	*Molothrus ater*	NAM	5.4		
House Finch	*Carpodacus mexicanus*	PER	4.1		3.9
American Goldfinch	*Carduelis tristis*	NAM	6.3		3.5
House Sparrow	*Passer domesticus*	PER	11.8		17.6

[a] Represents the absolute number of individuals.

The Wilson Journal of Ornithology 120(3):565–568, 2008

ECTOPARASITES AFFECT HEMOGLOBIN AND PERCENTAGES OF IMMATURE ERYTHROCYTES BUT NOT HEMATOCRIT IN NESTLING EASTERN BLUEBIRDS

RENEÉ E. CARLETON[1,2]

ABSTRACT.—Populations of the hematophagous mite, *Dermanyssus prognephilus*, within Eastern Bluebird (*Sialia sialis*) nests were manipulated using a pyrethrin-based insecticide to examine effects on nestling growth, selected hematological parameters, and fledging success. There was no difference in body mass, fledging success, estimated white blood cell counts, or hematocrits of infested versus non-infested nestlings. However, infested nestlings had a 25.0% reduction in hemoglobin and a 20.5% increase in immature erythrocytes. These findings suggest a physiological response to parasite feeding that may affect post-fledging survival. *Received 13 October 2007. Accepted 16 January 2008.*

Nestling birds are subject to a large number of ectoparasites, including hematophagous mites (Acari) (Møller 1990, Burtt et al. 1991, Richner et al. 1993). Direct effects of ectoparasites on nestlings have been studied frequently but often with contradictory conclusions (Møller 1990, Richner et al. 1993, Tompkins et al. 1996, O'Brien et al. 2001). Some studies concluded that nest infestations were associated with greater nestling mortality or smaller size and weight at fledging (Møller 1990, Richner et al. 1993). Tompkins et al. (1996) found no negative effects of ectoparasitism on nestling Common Swifts (*Apus apus*).

Many studies of effects of ectoparasites on nestling and fledgling survival focused on growth parameters (i.e., tarsus length and weight), but some examined hematological effects such as hematocrit (packed cell volume) and hemoglobin levels (Chapman and George 1991, Whitworth and Bennett 1992, O'Brien et al. 2001, Hannam 2006). For example, in a study comparing blood hemoglobin levels of House Wren (*Troglodytes aedon*) nestlings, parasitized nestlings had significantly lower hemoglobin levels. O'Brien et al. (2001) hypothesized parasite-mediated effects may have significant impacts on post-fledge survival by reducing flight ability due to blood loss and reduced oxygen availability.

Eastern Bluebird (*Sialia sialis*) nests are frequently infested with blood-feeding mites of the genus *Dermanyssus* (*D. hirundinis*, *D. prognephilus*) (Burtt et al. 1991, Mataxas and Pung 1999). Bluebirds readily accept wood nest boxes as replacements for naturally-occurring cavities (Zeleny 1977). Management of nest boxes, including leaving old nesting material in place, often results in large parasitic mite populations (Burtt et al. 1991). This practice could reduce nestling survival in populations dependent on artificial nesting sites if parasitism causes a negative impact to growth and condition. My objective was to investigate effects of a commonly occurring hematophagous nest mite (*Dermanyssus prognephilus*) on hematological and physical parameters of Eastern Bluebird nestlings by manipulation of mite populations within artificial nesting sites (wood nest boxes).

METHODS

Study Area.—The study occurred in the Ridge and Valley physiographic province of northwestern Georgia, USA (34° 28′ N, 85° 19′ W) during the 2006 breeding season (Mar–Aug). Study sites consisted of two, non-contiguous 40-ha areas which provided suitable bluebird habitat of grassy vegetation with perching sites and structures providing nesting opportunities (nest boxes).

Nestling Manipulation.—Nest boxes were constructed from unpainted white pine (*Pinus strobus*) lumber. All boxes had been in place since 2002 and contained bluebird nests in previous breeding seasons. Nest mites were regularly seen on nestlings and within recently fledged nests. I removed old nestling material each time a nest box was vacated from 2002 to 2006 to prevent large accumulations of

[1] Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30603, USA.

[2] Current address: Department of Biology, School of Mathematical and Natural Sciences, Berry College, Mount Berry, GA 30149 USA;
e-mail: rcarleton@berry.edu

mites. Fifteen nest boxes within each site were monitored for nesting activity beginning in early March 2006. Second broods of the season from nest boxes that fledged a brood earlier were selected for the study because those boxes were likely to contain numerous mites. Boxes with clutches consisting of at least three eggs were randomly assigned to either a control (no miticide application) or treatment (miticide application) group.

Two days before the estimated hatch date ~25 g of Johnson's Rid Mite Powder For Birds (Johnson's Veterinary Supply, UK), a pyrethrin-based miticide, were applied to treatment group nests after temporarily removing the eggs. This treatment was selected because pyrethrin is considered non-toxic to birds (Theodorides 1990). A minimum amount of powder yielding complete coverage was used on nests. Powder was reapplied to nests and nestlings were lightly dusted with ~5 g on day 3, 6, and 10 post-hatching. Nests and nestlings assigned to the control group were handled to simulate application of powder.

Three nestlings from treatment and control boxes containing broods of 3–5 nestlings were chosen at random for measurement on day 12 post-hatching. The number of nestlings per nest box was recorded. Individually numbered U.S. Geological Survey aluminum leg bands were placed on nestlings for identification. Body mass and right tarsus length were measured, and a 20-μl blood sample was obtained by jugular venipuncture. A small quantity of the sample was used to make a blood smear and fill one hematocrit tube. The blood smear was air-dried and stained with a Wright's-type stain (Hemacolor Staining Solution, EM Science, Gibbstown, NJ, USA). The remainder was placed in a vial containing anticoagulant for hemoglobin measurement and an estimated white blood cell count. Nestlings were examined for presence or absence of *D. prognephilus* or other species of hematophagous mites and other ectoparasites, such as lice or blow fly larvae (Diptera). Boxes were monitored for an additional 10 days to document fledging. All nests were removed from vacated boxes and visually examined by sifting through the nesting materials. I noted presence or absence of mites or other ectoparasites but elected not to quantify mite numbers.

Hematological Parameters.—I measured hemoglobin indirectly by colorimetric assay using a QuantiChrom Hemoglobin Assay Kit (BioAssay Systems Inc., Hayward, CA, USA). The assay was performed on 10 μl of whole blood diluted 100-fold with distilled water (Frank Huang, BioAssay Systems Inc.; pers. comm.). Absorbance at 400 nm of the hemoglobin standard supplied with the kit and the diluted sample was measured with a Spectronic 20D+ spectrophotometer (Thermo Electron Corp., Waltham, MA, USA). Hemoglobin absorbance of samples from individual nest boxes was standardized by dividing the absorbance of the sample by the absorbance of the standard. Hematocrit or packed cell volume (% packed red blood cells per blood volume) was measured using centrifuged whole blood in standard 50-μl capillary tubes and a Critocaps micro-hematocrit capillary tube reader (Oxford Labware, St. Louis, MO, USA).

The estimated white blood cell count (10^6 WBC/μl) was obtained using the Unopette 5877 system (Becton-Dickinson, Rutherford, NJ, USA), a Neubauer hemacytometer, and the stained blood smear. The estimated white blood cell count was calculated following Redig (1997). Percent polychromasia or number of polychromatic (immature) erythrocytes per 100 erythrocytes counted was measured using the stained blood smear examined at 1,000×. Polychromatic cells were differentiated from mature cells by the presence of a more basophilic cytoplasm and less condensed nuclear chromatin (Campbell 1995). Immature cells observed in this study were not designated as reticulocytes because a vital stain was not used. Mature erythrocytes may contain sufficient reticulum to appear as reticulocytes when stained with methylene blue (Dein 1986).

Statistical Analyses.—Hematological and physical parameter values of the three nestlings measured per nest box were used to calculate a mean value for each nest box. The mean nest box value was used as the unit of analysis to avoid pseudoreplication and negate individual differences among nestlings due to competition. A Shapiro-Wilk *W* Test was used to assess normality on all units before analyses. All data were normally distributed except for percent polychromasia which was square-root transformed. Group (control and treatment), site, and brood size (3, 4, or 5 nestlings) were included as main effects in the

TABLE 1. Mean (± SD) body mass, packed cell volume, estimated white blood cell count, hemoglobin absorbance, and percent polychromatic or immature erythrocytes of 12-day-old Eastern Bluebird nestlings raised in non-treated (control) vs. pyrethrin-treated (treatment) nest boxes in Georgia, 2006.

Parameter	Control (n = 10)	Treatment (n = 8)	$F_{1,18}$	P
Body mass, g	24.84 ± 2.03	25.66 ± 2.68	0.55	0.46
Hematocrit, %	43.9 ± 3.17	42.3 ± 3.39	0.89	0.36
Estimated WBC, 10^6 WBC/μl	86.9 ± 29.37	78.1 ± 26.38	0.05	0.82
Hemoglobin absorbance, nm[a, b]	1.2 ± 0.28	1.5 ± 0.24	10.64	0.006
Percent polychromatic cells[b]	39.0 ± 0.06	31.0 ± 0.53	6.23	0.028

[a] Square root transformed.
[b] $P < 0.05$.

original model; however, site and brood size were highly correlated. Site contributed relatively less to the r^2 value than brood size and was deleted from the final model. Body mass was analyzed using ANCOVA with tarsus length as the covariate. Hematological parameters were compared using an A × B factorial ANOVA. All analyses (*a priori* $\alpha = 0.05$) were performed using JMP IN 5.1 Statistical Software (SAS Institute Inc. 2003).

RESULTS

Sample Size.—Eighteen of 30 nest boxes monitored contained broods of 3 to 5 nestlings which survived predation for the duration of the study. All nestlings ($n = 69$) monitored fledged successfully. Eight boxes were assigned to the treatment group and 10 were assigned to the control group. Mites (*D. prognephilus*) were recovered from all control group nests. Nests treated with the miticide powder were free of mites and no other species of ectoparasites were recovered from control or treatment group nests.

Physical Parameters.—Neither treatment nor control group differed in body mass (Table 1). Brood size did not influence body mass.

Hematological Parameters.—There was no difference in main effects or interactions for estimated white blood cell count or hematocrit between nest boxes treated for mites and non-treated nest boxes (Table 1). The analysis revealed a significant main effect for group (treatment vs. control) for both hemoglobin absorbance and percent polychromasia (Table 1). There were no effects of brood size and no additive effects.

DISCUSSION

This study demonstrated a direct effect of pyrethrin application and blood loss on Eastern Bluebird nestlings and was the first to document an increased release of immature erythrocytes associated with parasite feeding on nestling birds. The increased numbers of immature erthrocytes in non-treated nestlings, as measured by percent polychromatic cells, was representative of a physiologic response to blood loss (Campbell 1995). Birds naturally possess a great capacity to maintain blood volume (Campbell 1995). This probably explains the lack of difference in control and treatment group packed cell volumes and the significant difference in percent polychromasia. The lower hemoglobin level is also indicative of blood loss in the non-treated nestlings. In a study examining the effect of blow fly larvae on nestling House Wrens, O'Brien et al. (2001) found reductions in hemoglobin levels but not hematocrits. Eastern Bluebird nestlings parasitized by blow flies also had similar reductions in hemoglobin but not hematocrit (Hannam 2006). Hematocrit appears to be a less reliable indicator of blood loss in birds than blood hemoglobin levels. Measuring percent of polychromatic cells in addition to blood hemoglobin should provide a more accurate assessment of ectoparasite effects.

Body mass was not affected by parasitism suggesting that either blood loss does not negatively impact growth or parasitized nestlings are able to sufficiently compensate physiologically. Estimated white blood cell counts were also not affected by parasitism which suggested no increase in immune response was elicted.

The lack of difference in fledging success of parasitized versus non-parasitized nestlings suggests that hematophagous mites had no direct effect on nestling mortality. Lope et al. (1993) indicated parasites and adverse envi-

ronmental conditions interact to negatively affect host condition. Favorable weather during the study may have contributed to the survival of parasitized nestlings.

Survival following fledging was not examined. Post-fledging survival of parasitized nestlings may be negatively affected by decreased flight capability resulting from blood loss and reduced hemoglobin levels (O'Brien et al. 2001). Fledgling bluebirds fly to the tops of trees upon leaving the nest and remain near or within cover for ~7 days (Gowaty and Plissner 1998). Fledglings with decreased flight capacity may be unable to reach cover or avoid predation until hemoglobin level normalizes with erythrocyte maturation.

Additional studies focusing on post-fledging survival of parasitized and non-parasitized nestlings would add greatly to our understanding of nest parasite-mediated effects on this and other species. Pyrethrin-based pesticides are acceptably safe for use on birds (Theodorides 1990) and treatment of vacated nest boxes following removal of old nesting material is recommended for reduction or elimination of residual mite populations.

ACKNOWLEDGMENTS

This study was supported by an H. Branch Howe Research Grant from the Georgia Ornithological Society. I thank D. B. Conn, J. H. Graham, D. A. Krause, E. D. Elsberry, and K. W. Wilson for access to the study site and use of facilities, P. A. Gowaty for her knowledge of bluebird behavior and under whose master permit banding was supervised, and H. C. Proctor for mite identification. I also thank S. H. Schweitzer, L. S. Johnson, and an anonymous reviewer for suggestions regarding the manuscript.

LITERATURE CITED

Burtt, E. H., W. Chow, and G. A. Babbitt. 1991. Occurrence and demography of mites of Tree Swallow, House Wren, and Eastern Bluebird nests. Pages 104–122 *in* Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M. Zuk, Editors). Oxford University Press, Oxford, United Kingdom.

Campbell, T. W. 1995. Avian hematology. Pages 3–19 *in* Avian hematology and cytology. Second Edition. Iowa State University Press, Ames, USA.

Chapman, B. R. and J. E. George. 1991. The effects of ectoparasites on Cliff Swallow growth and survival. Pages 69–92 *in* Bird-parasite interactions: ecology, evolution, and behaviour (J. E. Loye and M. Zuk, Editors). Oxford University Press, Oxford, United Kingdom.

Dein, F. J. 1986. Hematology. Pages 174–191 *in* Clinical avian medicine and surgery (G. J. Harrison and L. R. Harrison, Editors). W. B. Saunders Company, Philadelphia, Pennsylvania, USA.

Gowaty, P. A. and J. H. Plissner. 1998. Eastern Bluebird (*Sialia sialis*). The birds of North America. Number 381.

Hannam, K. 2006. Ectoparasitic blow flies (*Protocalliphora* sp.) and nestling Eastern Bluebirds (*Sialia sialis*): direct effects and compensatory strategies. Canadian Journal of Zoology 84:921–930.

Lope, F., G. Gonzalez, J. J. Perez, and A. P. Møller. 1993. Increased detrimental effects of ectoparasites on their bird hosts during adverse environmental conditions. Oecologia 95:234–240.

Mataxas, K. M. and O. Pung. 1999. Effects of endoparasites and hematophagous ectoparasites on reproductive success of Eastern Bluebirds (*Sialia sialis*). The Oriole 64:41–45.

Møller, A. P. 1990. Effects of parasitism by the haematophageous mite *Ornithonyssus bursa* on reproduction in the Barn Swallow (*Hirundo rustica*). Ecology 71:2345–2357.

O'Brien, E. L., B. L. Morrison, and L. S. Johnson. 2001. Assessing the effects of haematophagous ectoparasites on the health of birds: haemocrit vs. haemoglobin levels in House Wrens parasitized by blow fly larvae. Journal of Avian Biology 32:73–76.

Redig, P. 1997. Unopette method for indirect determination of the total white blood cell count (TWC) (Phloxine diluent). Page 1023 *in* Avian medicine and surgery (R. B. Altman, S. L. Clubb, G. M. Dorrestein, and L. Quesenberry, Editors). W. B. Saunders Company, Philadelphia, Pennsylvania, USA.

Richner, H., A. Oppliger, and P. Christe. 1993. Effect of an ectoparasite on reproduction in Great Tits. Journal of Animal Ecology 62:703–710.

SAS Institute Inc. 2003. JMP IN statistical analysis software. Release 5.1.2. SAS Institute Inc., Cary, North Carolina, USA.

Theodorides, V. J. 1990. Antiparasitic drugs. Pages 225–266 *in* Parasitology for veterinarians, Fifth Edition (J. R. Georgi and M. E. Georgi, Editors). W. B. Saunders Company, Philadelphia, Pennsylvania, USA.

Tompkins, D., T. Jones, and D. H. Clayton. 1996. Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*Apus apus*). Functional Ecology 10:733–740.

Whitworth, T. L. and G. F. Bennett. 1992. Pathogenicity of larval *Protocalliphora* (Diptera:Calliphoridae) parasitizing nestling birds. Canadian Journal of Zoology 70:2184–2191.

Zeleny, L. 1977. Song of hope for the bluebird. National Geographic 151:854–865.

The Wilson Journal of Ornithology 120(3):569–574, 2008

OBSERVATIONS ON FLOCKING BEHAVIOR OF WORTHEN'S SPARROWS (*SPIZELLA WORTHENI*) AND OCCURRENCE IN MIXED-SPECIES FLOCKS

JULIO C. CANALES-DELGADILLO,[1,3] LAURA M. SCOTT-MORALES,[1] MAURICIO COTERA CORREA,[2] AND MARISELA PANDO MORENO[2]

ABSTRACT.—Worthen's Sparrow (*Spizella wortheni*) is one of the most endangered species in Mexico. Its survival depends on appropriate conservation strategies and reliable information about the species. Our study on winter groups of Worthen's Sparrow flocking with other grassland bird species provides preliminary ecological and behavioral information on this species, and its relation to other migratory and resident bird species in La Perforadora Valley, Coahuila, Mexico. We observed flocking associations of Worthen's Sparrow with 16 other species. Ochiai's Association Coefficient indicated Worthen's Sparrow often associated with Vesper Sparrow (*Pooecetes gramineus*) (0.60), Black-throated Sparrow (*Amphispiza bilineata*) (0.33), Horned Lark (*Eremophila alpestris*) (0.27), and Western Bluebird (*Sialia mexicana*) (0.22). Worthen's Sparrow occurred more frequently in mixed than in monospecific flocks in winter. It foraged more frequently on the ground but also searched in shrub stems, branches, and foliage from perches, and at times hawked for flying insects from perches. Most perches were in the shrub stratum, but fences also were used. Worthen's Sparrow in mixed-species flocks spent more time in foraging activities than those in monospecific flocks. *Received 29 March 2007. Accepted 3 December 2007.*

The grasslands of northeastern Mexico, in the Mexican Plateau, support a great variety of resident and migratory bird species, flocking together in winter in heterospecific or monospecific groups. Flocking in grassland birds is an adaptive response to lack of vegetation cover and reduces niche overlap, avoids intraspecific aggression, improves likelihood of predator detection, and facilitates feeding (Powell 1979, Hutto 1994, Latta and Wunderele 1996). We studied the winter behavior of Worthen's Sparrow (*Spizella wortheni*) to learn more about the ecology of this endemic bird species of the Mexican Plateau. Habitat loss and fragmentation have contributed to classification of Worthen's Sparrow as one of the most threatened emberizid sparrows of the world (Wege et al. 1993, Behrstock et al. 1997, BirdLife International 2000). The objective of this paper is to describe flocking behavior and flock composition of Worthen's Sparrow, and to provide information that may contribute to development of effective conservation practices.

METHODS

Study Area.—The study was conducted in a 1,070-ha grassland valley, "La Perforadora" (Scott-Morales et al. 2004), in the State of Coahuila, México, 45 km south of Saltillo City (25° 03′ 52″ N, 100° 59′ 10″ W). The annual average temperature and rainfall in this area over the last 10 years was 17° C and 43.5 cm, respectively (Orta 1988, Rioja 2003). The vegetative ground cover ranged between 20 and 25%, and the grassland landscape was dominated by Hairy muhly (*Muhlenbergia villiflora* var. *villiflora*) associated with Buffalograss (*Buchloe dactyloides*) and Burrograss (*Scleropogon brevifolius*). A rosette scrub develops at the edge of the grassland in coarser soils dominated by Giant Spanish Dagger (*Yucca carnerosana*), Texas sotol (*Dasylirion texanum*), Cortadillo (*Nolina cespitifera*), Lechuguilla (*Agave lechuguilla*), and Espadin (*A. striata*) with woody plant cover rarely exceeding 15% (Rioja 2003).

Field Observations.—We searched intensively for Worthen's Sparrow flocks during January to November 2005 from 0630–0700 to 1200 hrs and from 1600 to 1800 hrs CST. Observers searched the study area starting

[1] Facultad de Ciencias Forestales, Departamento de Ciencias Básicas, Universidad Autónoma de Nuevo León, Carretera Nacional Km 145, C.P. 67700, Linares, Nuevo León, México.

[2] Facultad de Ciencias Forestales, Departamento Agroforestal, Universidad Autónoma de Nuevo León, Carretera Nacional Km 145, C.P. 67700, Linares, Nuevo León, México.

[3] Corresponding author; e-mail: cadj0506@yahoo.com.mx

from randomly chosen cardinal directions. If Worthen's Sparrows were absent in a flock, the search was resumed to locate the next flock (Ralph et al. 1996, Villaseñor and Santana 2003). We registered the initial and final position of each flock containing Worthen's Sparrows using GPS.

Each focal flock was followed as long as possible and the following information was recorded: number of individual Worthen's Sparrows, activities, and positions in the vegetation. We observed focal individuals for activities and randomly selected five individuals from each flock to examine position in the vegetation. We recorded for each individual, after 5 min of visual contact to minimize the influence of the observers on its behavior, the first position in the vegetation. We registered position in relation to four vegetation strata (Moreno 1984): grasses <2–5 cm in height or bare ground (ground); non-woody plants between 5 and 40 cm in height (herbaceous stratum); woody perennial plants <3 m high, branched at the base (shrub stratum); and woody perennial plants >3 m high, not branched at the base (arboreal stratum).

Flock Composition.—We measured coexistence between Worthen's Sparrows and other species in the flocks. Coexistence of species was calculated using Ochiai's Similarity Coefficient $r_o = A/[\sqrt{A + B} \cdot \sqrt{A + C}]$, where A is the number of places where species one and species two were found, B is the number of places where species one has been found but not species two, and C is the number of places where species two has been found but not species one. This coefficient provides information about co-occurrence of two species in the same area or locality in the range 0 to 1.0 (Janson and Vegelius 1981, Jackson et al. 1989). Assuming that r_o is approximately normally distributed with the mean, asymptotic standard error was calculated as: $\hat{\sigma}^2(r_o) = (a^2c + a^2b + 4abc)/[4(a + b)^2 \cdot (a + c)^2 \cdot n] \Rightarrow \hat{\sigma}(r_o)$, where a, b, and c are proportions obtained from division of A, B, and C by n that, in this case, is the total number of flocks.

We quantified foraging and vigilance time of Worthen's Sparrows in both heterospecific and monospecific flocks. We randomly selected a focal individual (following Austin and Linwood 1972) and observed it for 3 min, recording foraging and vigilance activity. Foraging (food-search) and food-capture behaviors were treated as feeding activity while vigilance was measured as time spent looking around from the ground or perches. We used t-tests to compare mean group size, and mean foraging and vigilance times in both types of flocks; mean values are reported with ± standard error. We used a one-way ANOVA to compare size of monospecific and heterospecific flocks between breeding and non-breeding seasons using Statistica Kernel release 5.1 (StatSoft Inc. 1998).

RESULTS

We observed 245 bird flocks along 49 transects including 64 mixed-species flocks and 182 monospecific flocks. Worthen's Sparrows occurred in 27 (43%) mixed flocks and 19 (10%) monospecific flocks. The average number of species in mixed flocks containing Worthen's Sparrows was 2.7 ± 1.19 per flock and mean flock size was 12.9 ± 8.97 birds (range 3–31). Mean group size in monospecific flocks of Worthen's Sparrows was 10.7 ± 8.81 individuals per flock (range 2–30). We found no difference between mean sizes of monospecific and heterospecific flocks ($t_{44} = -0.81$, $P = 0.42$).

Worthen's Sparrows associated with 16 other species in heterospecific flocks (Table 1). Based on Ochiai's Similarity Coefficient, the highest values of coexistence between Worthen's Sparrows and species in the mixed flocks were Vesper Sparrows (*Pooecetes gramineus*) (0.60), Black-throated Sparrows (*Amphispiza bilineata*) (0.33), Horned Lark (*Eremophila alpestris*) (0.27), and Western Bluebird (*Sialia mexicana*) (0.22).

The breeding season in our study area occurred from mid-April to late August. Monospecific and mixed-species flocks were observed in both breeding and non-breeding seasons. We recorded five monospecific and seven heterospecific flocks during the breeding period, and 14 monospecific and 20 heterospecific flocks during the non-breeding period. A one-way ANOVA indicated that mean flock size in the two types of flocks did not differ ($F_{3,42} = 2.331$, $P = 0.0879$) between breeding and non-breeding seasons (Fig. 1). Flocking incidence was higher during the non-breeding season than during either the breeding season

TABLE 1. Coexistence coefficient ± asymptotic SE for Worthen's Sparrow and associated species in mixed-species flocks.

Species	Scientific name	Ochiai's Similarity Coefficient
Black-throated Sparrow	*Amphispiza bilineata*	0.33 ± 0.23
American Pipit	*Anthus rubescens*	0.19 ± 0.24
House Finch	*Carpodacus mexicanus*	0.21 ± 0.22
Lark Sparrow	*Chondestes grammacus*	0.20 ± 0.25
Yellow-rumped Warbler	*Dendroica coronata*	0.17 ± 0.25
Horned Lark	*Eremophila alpestris*	0.28 ± 0.25
Northern Mockingbird	*Mimus polyglottos*	0.10 ± 0.22
Canyon Towhee	*Pipilo fuscus*	0.20 ± 0.25
Vesper Sparrow	*Pooecetes gramineus*	0.60 ± 0.22
Rock Wren	*Salpinctes obsoletus*	0.27 ± 0.24
Say's Phoebe	*Sayornis saya*	0.09 ± 0.20
Western Bluebird	*Sialia mexicana*	0.23 ± 0.22
Clay-colored Sparrow	*Spizella pallida*	0.19 ± 0.24
Chipping Sparrow	*S. passerina*	0.15 ± 0.23
Field Sparrow	*S. pusilla*	0.29 ± 0.25
Curve-billed Thrasher	*Toxostoma curvirostre*	0.09 ± 0.20

or the entire season for both monospecific and mixed-species flocks (Fig. 2). Flocks of both types were virtually absent from June to August when reproductive activity of Worthen's Sparrows was high (Fig. 3) and single males or pairs were prevalent. During September we found only three pairs of Worthen Sparrows.

Foraging occurred most frequently on the ground (76%) and the herbaceous stratum received less attention by birds (4%). Worthen's

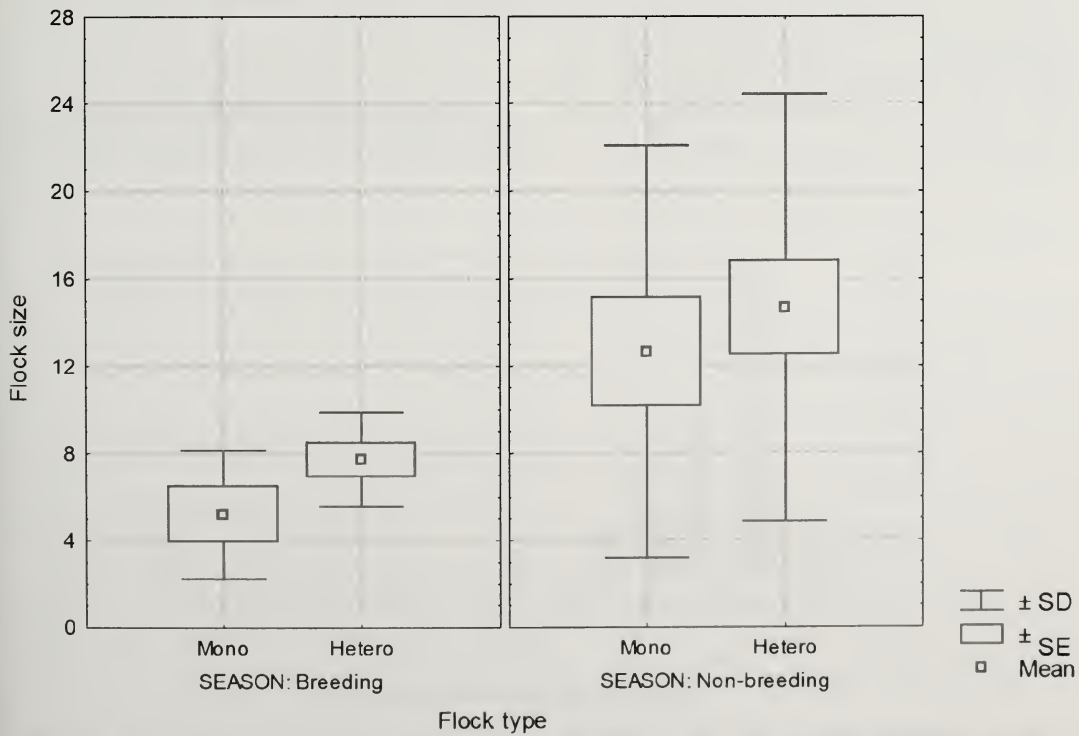


FIG. 1. Flock size of Worthen's Sparrow (monospecific flocks = mono) and mixed-species (heterospecific flocks = hetero) in the breeding and non-breeding seasons in Coahuila, Mexico.

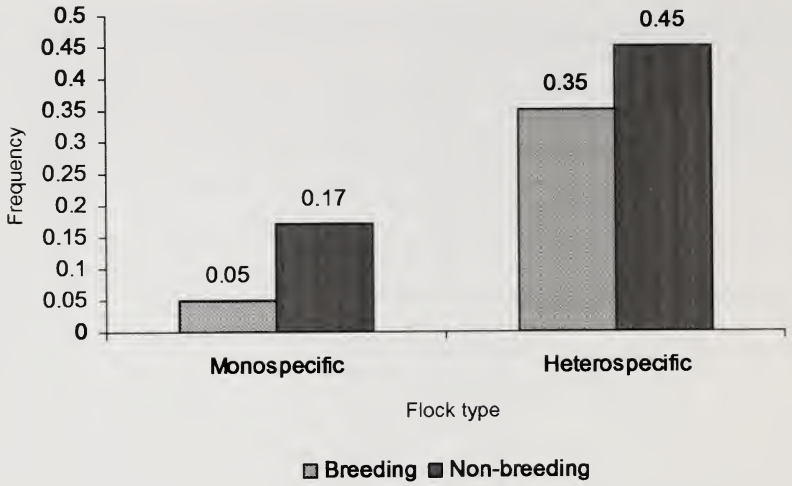


FIG. 2. Flocking incidence of Worthen's Sparrow during the breeding and non-breeding season by flock type. Numbers above the bars are the frequency values of Worthen's Sparrows in each type of flock.

Sparrows also searched shrub stems, branches, and foliage from perches, and at times hawked for flying insects from these perches. Most perches were in the shrub stratum (87%), but fences also were used (12%).

We observed foraging behavior in 41 and 39 focal individuals of Worthen's Sparrow in monospecific and heterospecific flocks, respectively. Sparrows in monospecific and mixed species flocks differed strongly in foraging time, spending an average of 27.0 ± 27.73 sec (n = 33) and 69.2 ± 46.11 sec (n = 38), respectively ($t_{78} = -4.98$, $P < 0.000$). However, we found no difference ($t_{78} = 1.9$, $P = 0.06$) in vigilance times with an average vigilance time of 32.5 ± 39.60 sec by individuals in both monospecific and mixed flocks.

DISCUSSION

Our observations confirm monospecific flocking by Worthen's Sparrows (Wege et al.

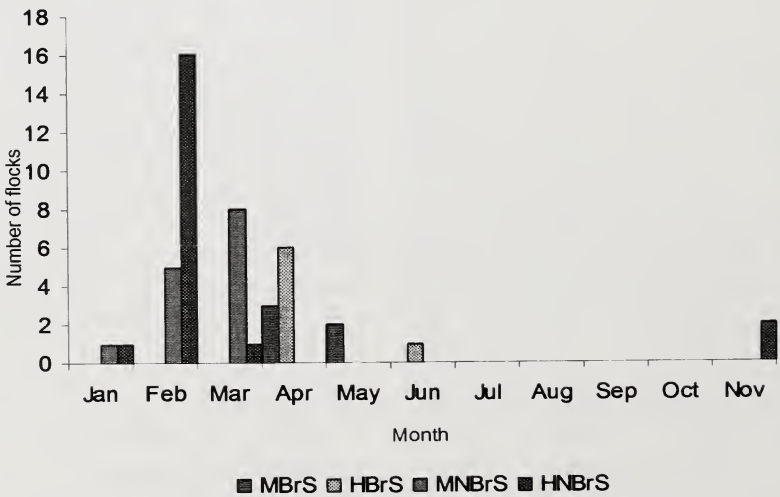


FIG. 3. Flocking incidence of Worthen's Sparrow during the breeding (MBrS = monospecific flocks; HBrS = heterospecific flocks) and non-breeding seasons (MNBrS = monospecific flocks; HNBrS = heterospecific flocks).

1993, Behrstock et al. 1997), but also reveal the species commonly occurs in mixed species flocks in the non-breeding season. We found Worthen's Sparrows occurred more often in heterospecific than in monospecific flocks.

Flocking incidence of Worthen's Sparrows decreased in late winter and early spring, as reported by Powell (1979), who found the largest flock sizes among neotropical birds occurred from November to February. The decrease in flocking incidence during the breeding season and flocking associations with 16 species, some of which are migratory species, suggest that flocking in Worthen's Sparrows was seasonal and that flock composition becomes more heterogeneous with inclusion of migrants. Our data showed a flocking incidence of 35% in mixed-species flocks during the breeding season, but most of these observations were recorded early in the breeding season when flocks were starting to disperse.

Most species that coexist with Worthen's Sparrows in heterospecific flocks had similar food habits, feeding mainly on insects and seeds (Austin and Linwood 1972). Moreover, some species used the same foraging technique, searching systematically for food across the study area. Powell (1979) and Hutto (1994) reported that some species in heterospecific bird flocks obtain food from the activities of others. Waite and Grubb (1988) reported similar behavior in mixed-species bird flocks of temperate-deciduous woodlands.

Worthen's Sparrows closely associated with Vesper Sparrows, which is a migratory species that winters in our study area. Gram (1998) suggested the association between resident and migrant neotropical species in northeastern Mexico has an important winter survival function. Thus, migrant species in our study area could be joining opportunistically with resident species to derive survival benefits in winter. This may be one reason for the strong association with Vesper Sparrows.

We frequently witnessed cases of alarm signaling by flock associates (e.g., Western Bluebirds, Vesper Sparrows, Yellow-rumped Warblers [*Dendroica coronata*]) feeding with Worthen's Sparrows in mixed flocks. Others have emphasized the importance for ground-foragers of collective vigilance provided by many individuals and several species foraging together in mixed groups (e.g., Powell 1979, Goldman 1980, Hutto 1994, Latta and Wunderele 1996, Benkman 1997, Gram 1998, Dolby and Grubb 1999).

ACKNOWLEDGMENTS

The research was funded by CONACYT (C01-0700), the University of Nuevo León (CN 926-04), and The Nature Conservancy (MBP/PW 010703). We thank Nick Reid, Celina Garza, and Regina Pérez for helping with revision and comments on this paper, and Claudia Doria Treviño, Leonel Reséndiz, and Rogelio Hernández for helping process data and with field work.

LITERATURE CITED

Austin, G. T. and E. Linwood. 1972. Winter foraging ecology of mixed insectivorous bird flocks in oak woodland in southern Arizona. Condor 74:17–24.

Behrstock, R. A., C. W. Sexton, G. W. Lasley, T. L. Eubanks, and J. P. Gee. 1997. First nesting records of Worthen's Sparrow (*Spizella wortheni*) for Nuevo León, México, with habitat characterization of the nest site and notes on ecology, voice, additional sightings and leg coloration. Cotinga 8:27–33.

Benkman, C. W. 1997. Feeding behavior, flock size-dynamics, and variation in sexual selection in crossbills. Auk 114:163–178.

BirdLife International. 2000. Threatened birds of the world. Lynx Editions and BirdLife International, Barcelona, Spain and Cambridge, United Kingdom.

Dolby, A. S. and T. C. Grubb Jr. 1999. Functional roles in mixed-species foraging flocks: a field manipulation. Auk 116:557–559.

Goldman, P. 1980. Flocking as possible predator defense in Dark-eyed Juncos. Wilson Bulletin 92: 88–95.

Gram, W. K. 1998. Winter participation by neotropical migrant and resident birds in mixed-species flocks in northeastern Mexico. Condor 100:44–53.

Hutto, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in western Mexico. Condor 96: 105–118.

Jackson, D. A., K. M. Somers, and H. H. Harvey. 1989. Similarity coefficients of co-occurrence and association or simply measures of occurrence? American Naturalist 133:436–453.

Janson, S. and J. Vegelius. 1981. Measures of ecological association. Oecologia 49:371–376.

Latta, S. C. and J. M. Wunderele. 1996. The composition and foraging ecology of mixed-species flocks in pine forests of Hispaniola. Condor 98: 595–607.

Moreno, P. N. 1984. Glosario botánico ilustrado. Instituto Nacional de Investigaciones sobre Recursos Bióticos. Xalapa, Veracruz, México.

Orta, D. M. 1988. Influencia del Perrito de las praderas (*Cynomys mexicanus*) en la vegetación del suelo y pastizal mediano abierto en Coahuila. Thesis. Universidad Autonoma Agraria Antonio Narro, Saltillo, Coahuila, Mexico.

Powell, G. V. N. 1979. Structure and dynamics of interspecific flocks in a neotropical mid-elevation forest. Auk 96:375–390.

Ralph, C. J., G. R. Geupel, M. Pyle, T. E. Martin, D. F. Desante, and B. Milá. 1996. Manual de Métodos de Campo para el Monitoreo de Aves Terrestres. USDA, Forest Service, General Technical Report PSW-GTR-159-Web.

Rioja, P. T. M. 2003. Comportamiento reproductivo del perrito llanero (*Cynomys mexicanus*) en el Altiplano Mexicano. Thesis. Facultad de Ciencias Forestales, Universidad Autonoma de Nuevo Leon, México.

Sada, A. M. 1987. Locations for finding Worthen's Sparrow (*Spizella wortheni*) in Nuevo León [Coahuila]. MBA Bulletin Board 1(87–3):2.

Scott-Morales, L., E. Estrada, F. Chávez-Ramírez, and M. Cotera. 2004. Continued decline in geographic distribution of the Mexican prairie dog (*Cynomys mexicanus*). Journal of Mammalogy 85: 1095–1101.

StatSoft Inc. 1998. STATISTICA for Windows. Tulsa, Oklahoma, USA.

Villaseñor, G. J. F. and E. Santana C. 2003. El monitoreo de poblaciones: herramienta necesaria para la conservación de aves en México. Pages 224–262 *in* Conservación de Aves, Experiencias en México (H. Gómez de Silva and I. A. Oliveras, Editors). CONABIO, D.F., México.

Waite, T. A. and T. C. Grubb Jr. 1988. Copying of foraging locations in mixed-species flocks in temperate-deciduous woodland birds: an experimental study. Condor 90:132–140.

Wege, D. C., S. N. G. Howell, and A. M. Sada. 1993. The distribution and status of Worthen's Sparrow *Spizella wortheni*: a review. Bird Conservation International 3:211–220.

The Wilson Journal of Ornithology 120(3):575–581, 2008

STATUS OF CRESTED PENGUIN (*EUDYPTES* SPP.) POPULATIONS ON THREE ISLANDS IN SOUTHERN CHILE

DAVID A. OEHLER,[1,8] STEVE PELIKAN,[2] W. ROGER FRY,[3] LEONARD WEAKLEY JR.,[4] ALEJANDRO KUSCH,[5] AND MANUEL MARIN[6,7]

ABSTRACT.—We surveyed the coast of Chile between Isla Terhalten (54° 20′ S) and Islote Leonard (55° 44′ S) by boat during November–December 2005 to document breeding locations of Rockhopper (*Eudyptes chrysocome chrysocome*) and Macaroni (*E. chrysolophus*) penguins, and to count the number of nests during the early incubation period. A yacht-based observation recorded 1,000 Rockhopper Penguin nests at Isla Terhalten. Ground-based counts at Isla Noir estimated a total of 158,200 Rockhopper and 3,470 Macaroni penguin nests in 17 mixed colonies and one Macaroni Penguin breeding colony. The Rockhopper population on Isla Noir increased significantly from the previous estimate of 70,000 pairs, making this island the most important breeding site for the southern subspecies of Rockhopper Penguin. The new estimate for Rockhopper Penguins suggests a population increase over the last 20 years, consistent with recent data for the main colony in Argentina. Conservation status of the species and the factors potentially responsible for population declines elsewhere may need to be re-evaluated. *Received 11 July 2007. Accepted 9 December 2007.*

The Southern Rockhopper Penguin (*Eudyptes chrysocome chrysocome*) and Macaroni Penguin (*E. chrysolophus*) are the most numerous of the *Eudyptes* penguins (Woehler 1993, Reilly 1994). Both species have been classified as Vulnerable, based on declining populations of at least 30% over the last 30 years and continued anthropogenic pressures (e.g., fisheries activities and changes in the marine environment), by the International Union for the Conservation of Nature (IUCN)/ BirdLife International Red List (BirdLife International 2007a).

The world population of the Southern Rockhopper Penguin subspecies has been estimated at 475,000 breeding pairs at 51 sites in Argentina, Chile, and the Falkland Islands (Bingham and Majias 1999). Macaroni Penguins occur in at least 216 colonies at 50 breeding sites on many islands throughout subantarctic and Antarctic waters north of the pack ice. The world population estimate for the Macaroni Penguin is 9.0 to 11.7 million breeding pairs (Reilly 1994, Bingham and Majias 1999, BirdLife International 2007b). Long-term monitoring of these breeding sites shows a substantial decline in these populations over the last 50 years (Woehler and Croxall 1997; Barlow et al. 2002; Clausen and Huin 2003; Crawford et al. 2003, 2006; Pütz et al. 2003). Recent surveys in Argentina, involving the inventory of 180,000 pairs of Rockhopper Penguins on Staten Island, suggest the Bahía Franklin colony has dramatically increased from a few thousand pairs to 167,000 pairs and may indicate a geographical shift of birds from the Falkland Islands (Schiavini 2000). The number of Southern Rockhoppers in Chile was estimated at 175,000 pairs with the largest colonies of 70,000 and 13,000 pairs on Isla Noir and Diego Ramirez islands, respectively, but with no comprehensive monitoring to identify long-term trends (Venegas 1984, 1991; Woehler 1993). Recent studies indicate the Diego Ramirez population comprises 132,721 Rockhopper Penguin pairs (Kirkwood et al. 2007). The colony on Isla Noir of 70,000 pairs contains an estimated 35% of the total number along the coast of Chile (Venegas 1998).

The available data on total numbers and population trends of Southern Rockhopper Penguins in the Falkland Islands and along the coast of Argentina are more complete than data for Chilean populations. The Falkland Is-

[1] Feather Link Incorporated, Cincinnati, OH 45244, USA.

[2] University of Cincinnati, Math Department, MLO 025, Cincinnati, OH 45221, USA.

[3] 7920 Brill Road, Cincinnati, OH 45243, USA.

[4] 6613 Wyndwatch Drive, Cincinnati, OH 45230, USA.

[5] Casilla 19, Punta Arenas, Chile.

[6] Section of Ornithology, Natural History Museum of Los Angeles County, Los Angeles, 900 Exposition Boulevard, Los Angeles, CA 90007, USA.

[7] Current address: Casilla 15 Melipilla, Chile.

[8] Corresponding author;
e-mail: david.oehler@fuse.net

land Seabird Monitoring Programme, initiated in 1986/1987, has provided annual documentation of numbers and breeding success of penguins in the Falkland Islands (Thompson 1993, Pütz et al. 2003). These estimates have been based on quadrat sampling to equate occupied nest densities with measurements of the total area of the colonies (Schiavini 2000).

Inventories of Southern Rockhopper colonies in Chile have been sporadic or yacht-based (Woehler 1993). More in-depth quadrat sampling may be hampered by limited access to outlying islands. Nesting habitats used by penguin colonies, often on steep or heavily vegetated areas, makes direct observations of nests difficult without disruption of the colonies (Downes et al. 1959, Pütz et al. 2003). Woehler's (1993) reports of 100,000 pairs on the Ildefonso Group, 10,800 pairs on Barnevelt Island, and 3,000 pairs on Terhalten Island are estimates of adult birds accurate only to the nearest order of magnitude and were derived from Gerry Clark's expedition (Clark 1988). The IUCN established a high priority recommendation for the Southern Rockhopper Penguin, which included identification of the status and trends in Argentina, Chile, Falkland Islands/Malvinas (Ellis et al. 1998).

Macaroni Penguin populations along South America may be stable although sufficient data are lacking to identify trends (BirdLife International 2007b). Small colonies of Macaroni Penguins have been reported on Cabo Pilar, Isla Desolacion, Isla Diego Ramirez, Isla Deceit, Isla Terhalten, and Isla Recalada, Chile (Araya and Millie 1986, Wallace 1991). The population on Isla Recalada declined from 559 in 1989 to 421 in 1990 with no Macaroni Penguins observed in 1991 and 2005 (Soto 1990, Venegas 1991, Venegas and Soto 1992, Oehler et al. 2007). The total number of pairs on Isla Noir has been estimated at 12,500 to 25,000 (Venegas 1984, Woehler 1993).

The objectives of our survey were to (1) estimate the numbers of breeding Rockhopper and Macaroni penguins within the study areas (Fig. 1), and (2) establish a more accurate baseline population estimate to track future demographic trends, using direct counts in open areas and stratified random sampling in areas of heavy vegetation.

METHODS

We surveyed known locations of Rockhopper and Macaroni penguin colonies at Isla Noir (54° 20′ S, 73° 01′ W) from 8 through 25 November 2005 using maps and Global Positioning System (GPS) coordinates from previous studies. We conducted coastal searches, based on historic data for reference, by boat to expand the survey to adjacent islands. The goal was to collect data from each colony site to estimate total penguin populations. Study sites on Isla Noir and Islote Leonard (53° 23′ S, 74° 04′ W) demonstrated the timing of our survey coincided with peak colony attendance for the two species. Observations on penguins at Isla Terhalten (55° 26′ S, 67° 04′ W) on 22 December 2005 were limited to yacht-based counts. Investigators on Isla Noir and Islote Leonard conducted land-based systematic sampling of all geographic areas known to be used by penguins as described by Venegas (1984, 1991, 1998), Soto (1990), and Venegas and Soto (1992).

Direct ground counts were used only in areas where all birds within a colony could be observed completely, on Islote Leonard on 14 November 2005 and in the main Macaroni Penguin colony at Isla Noir on 9 November 2005. Three observers conducted simultaneous but independent counts of each area. The counts were repeated if any of the three counts for any given colony varied by more than 10% from the others. Each count was recorded separately.

We used quadrat sampling to estimate abundance (Krebs 1999) in areas of irregular topography and dense vegetation that precluded methodology developed for estimating breeding population size through use of ground counts (CCAMLR 1999). We conducted quadrat sampling on Isla Noir from 8 to 12 November 2005 in seven colonies selected at random from the 17 Rockhopper colonies. We delineated the outer perimeter of quadrats with yellow twine to facilitate plotting of nests. We recorded the total number of occupied penguin nests and nests with eggs in 45 randomly located 10 × 20-m quadrats within the Rockhopper colonies and 10 randomly located quadrats outside the colonies. We described habitat features within the quadrats, including vegetation type, soil, topography, el-

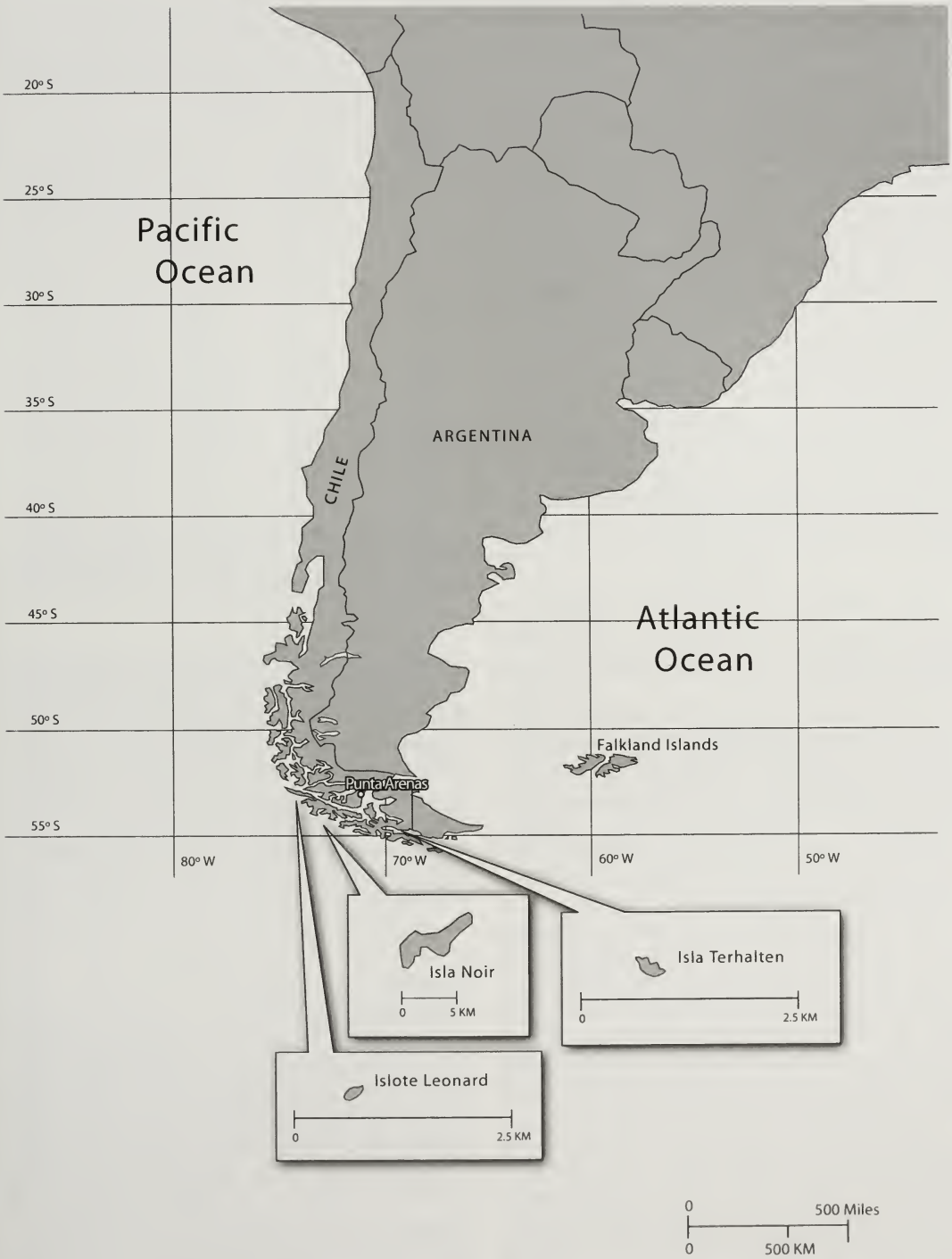


FIG. 1. Islote Leonard, Isla Noir, and Isla Terhalten along the coast of Chile.

evation, and slope. We manually recorded GPS waypoints at ~20-m intervals along the outer perimeter of all colonies to calculate the area of the colonies.

The area of the 17 accessible Southern Rockhopper Penguin breeding sites on Isla Noir was calculated from GPS coordinates and elevations using the GIS program AutoCAD. The variability in the estimate of the total density of nests can be attributed almost entirely to the variation due to sampling based on a conservative estimate of the coefficient of variation for the measurement of area (Bogaert et al. 2005). We choose to ignore the variability in the GPS measurement of the colony areas. The density of nests was calculated following Krebs (1999, 2002; C. J. Krebs, pers. comm.). We used confidence intervals for quantifying uncertainty of our density estimates (Krebs 1999).

RESULTS

Isla Terhalten—Rockhopper Penguin.—A yacht-based census estimated ~1,000 Rockhopper Penguin nests within the colony on Isla Terhalten.

Islote Leonard—Macaroni Penguin.—The survey documented a previously unrecorded colony of Macaroni Penguins on Islote Leonard (6.4 nautical km southeast of Isla Recalada). Direct counts recorded 132 (± 4 SD) occupied nests and 96% of Macaroni Penguins on nests were incubating with the remaining pairs attending empty nests.

Isla Noir—Rockhopper Penguin.—The total area of all colonies was 31.61 ha producing a population estimate of 158,200 (95% CI = 139,716–176,700) Rockhopper Penguin pairs for all colonies combined (Table 1). Pairs at occupied nests in the random quadrats within the colonies were incubating eggs (98%) with the remainder attending empty nests.

The number of nests per quadrat did not differ between colonies (Fig. 2; one-way ANOVA: $F = 0.99$, df = 6, $P = 0.45$) and we pooled data from all censused quadrats to estimate the number of penguins in the colonies. The variance-mean ratio test ($\chi^2 = 668.8$, df = 44; Krebs 1999:119) indicated that nests were more clustered ($P < 0.0001$) than they would be if spatially random. The counts produced parameter estimates $\mu = 100.11$ and $k = 4.257$ by fitting a negative binomial distribution (following Krebs 1999: equation 4.14). A $\log(x + k/2)$ transformation generated a 95% confidence interval of 88.4–111.8 for the number of nests per 200-m² quadrat. A Chi-square goodness-of-fit test ($\chi^2 = 18.334$, df = 12, $P = 0.11$) provided additional support for the negative binomial distribution.

TABLE 1. Rockhopper Penguin colonies on Isla Noir, November 2005. Areas of individual colonies and estimated total nests based on 95% confidence intervals for density of nests.

Rockhopper colony	Area (ha)	Estimated nests (95% CI)
1	0.39	1,953 (1,724–2,180)
2	1.35	6,757 (5,967–7,547)
3	1.34	6,706 (5,923–7,491)
4	3.45	17,267 (15,249–19,286)
5	3.23	16,166 (14,277–18,056)
6	0.25	1,251 (1,105–1,398)
7	1.41	7,057 (6,232–7,882)
8	0.35	1,752 (1,547–1,957)
9	5.63	28,177 (24,885–31,472)
10	1.06	5,305 (4,685–5,925)
11	2.80	14,013 (12,376–15,651)
12	4.29	21,471 (18,962–23,981)
13	0.58	2,903 (2,564–3,242)
14	0.75	3,754 (3,315–4,193)
15	1.15	5,756 (5,083–6,429)
16	1.36	6,807 (6,011–7,602)
17	2.22	11,111 (9,812–12,410)
Totals	31.61	158,200 (139,716–176,700)

Rockhopper Penguin nests were almost exclusively in tall grasses and most nests were associated with *Anthoxanthum redolens*. Nests were rarely found in wet areas containing other dominant vegetation such as *Iocenes acanthifolius* or in areas containing trees (e.g., *Nothofagus antarctica*).

Isla Noir—Macaroni Penguin.—We used the quadrat data from the Rockhopper Penguin census to estimate a total of 1,649 (95% CI = 386–2,913) Macaroni Penguin nests within the Rockhopper colonies. Macaroni Penguin nests were not spatially distributed randomly based on a variance-to-mean ratio test ($\chi^2 = 312.33$, df = 45, $P < 0.00001$). A negative binomial distribution best described the census data ($\chi^2 = 3.49$, df = 3, $P = 0.32$) with $\mu = 1.0435$ and $k = 0.193$. These population parameter estimates produce a 95% confidence interval for the number of nests/200-m² quadrat of 0.244–1.843.

Direct counts in the main Macaroni Pen-

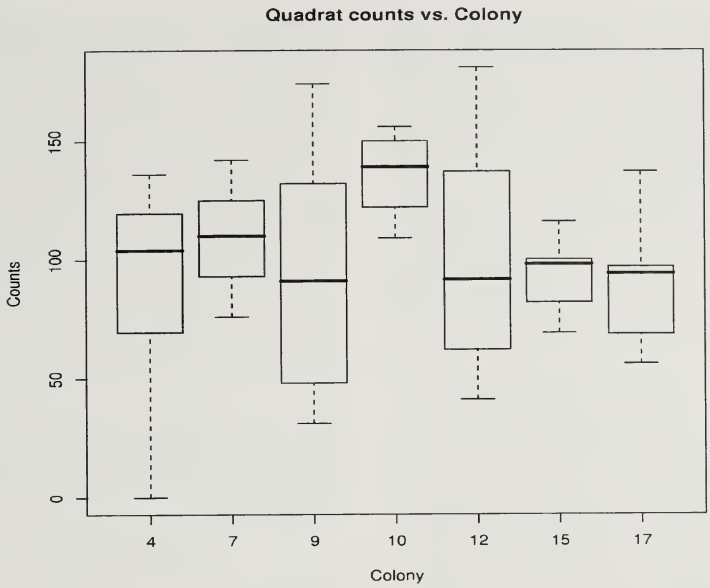


FIG. 2. Rockhopper Penguin nests per quadrat in seven randomly selected colonies on Isla Noir. Median counts per quadrat are indicated by thick solid lines, boxes indicate interquartile range, and thin solid lines represent minimum and maximum values.

guin colony on Isla Noir, recorded 1,816 (± 55 SD) occupied nests. We documented 3,470 (2,157–4,784) Macaroni Penguin nests on Isla Noir including those within the Rockhopper colonies. All Macaroni Penguins on nests within the mixed colonies were incubating eggs. Penguins (96%) within the main Macaroni colony were incubating eggs on nests and the remaining pairs were attending empty nests.

DISCUSSION

We describe a new colony of Macaroni Penguins on Islote Leonard with a relatively small population of 132 breeding pairs. The absence of historical data precludes clear interpretation of the findings, although with disappearance of the former colony on Isla Recalada (Oehler et al. 2007), these baseline data may suggest a possible shift from Isla Recalada to Islote Leonard.

The yacht-based survey of Isla Terhalten documented fewer Rockhopper Penguins than in past surveys. However, it is premature to draw conclusions from the current yacht-based observations in reference to historical accounts. Further land-based counts are required to more accurately describe population trends of Rockhopper and Macaroni penguins at this site.

This study represents the first complete inventory of Rockhopper Penguin numbers on Isla Noir through direct observation of each individual colony using standardized methodology. Population trends of the Southern Rockhopper Penguin on Isla Noir appear to mirror documented increases along the coast of Argentina (Schiavini 2000). Previously published estimates of 70,000 pairs of Southern Rockhopper Penguins on Isla Noir (Venegas 1984) are significantly lower than the 158,200 (139,716–176,700) pairs of Rockhoppers present in November 2005. However, site inventories by Venegas (1984) did not encompass the entire island and occurred during the later portion of the breeding season (Dec). Inability to access all colonies and attrition due to nest failure could partially account for the lower counts in 1983. The initial survey by Venegas (1984) described a significant population of Southern Rockhopper Penguins on Isla Noir, but those results may have underestimated population size and cannot reliably be used to demonstrate an increase in the population since 1983.

We cannot definitively conclude, based on

past estimates, the Rockhopper Penguin population on Isla Noir has increased in numbers in the last 20 years. However, evidence exists of the physical expansion of colonies through modifications in vegetation. The Rockhopper colonies along the coast of Isla Noir were similar in structural characteristics. Colony expansion into boundary areas containing trees, such as *Nothogagus antarctica*, may cause a reduction of *N. antarctica*, creating suitable conditions for succession of grass taxa. Correlation of active nests and weak or dead *N. antarctica* could demonstrate an expansion of the Rockhopper colonies and the related vegetation within the study sites, due to associated edaphic disturbances similar to those documented in seabird colonies (Ellis 2005).

Evaluation of the remaining Southern Rockhopper Penguin colonies should continue where past estimates were yacht-based and lack accuracy. Continued evaluation of the numbers of penguins on Isla Noir should also be conducted to better refine the estimated numbers and to document trends. Past estimates did not use appropriate methodologies and provided incomplete estimates of the penguin populations. Our census results provide suitable baseline data for future studies and could be used to review the conservation status of the subspecies, and factors potentially responsible for population declines elsewhere.

These data support designation of Isla Noir as an important nesting area for Southern Rockhopper Penguins. Sustainable management of Isla Noir for nesting Rockhoppers would require additional legal protection for the island. Developing a management plan will require detailed information on the population and further study of the biology of the penguins, including foraging areas and population recruitment. Isla Noir is presently not within Chile's park system, it lacks statutory protection, and is not monitored as closely as other areas containing penguin colonies. Management of Isla Noir would offer future protection for the existing population of Rockhoppers and provide a favorable breeding site that may attract birds from regions where populations are under adverse pressures.

ACKNOWLEDGMENTS

We thank the reviewers and editor for helpful comments on this manuscript. This work was supported through Feather Link, Inc. by grants-in-aid for scientific research from local and international foundations. We thank Brian and Holly Hunt of African Safari Wildlife Park, Indianapolis Chapter of the American Association of Zoo Keepers, Faunia, Cincinnati Zoo and Botanical Garden, and the Wave Foundation of the Newport Aquarium for financial support of this and past expeditions. We also thank Bob Brinkman at Woolpert LLP for assistance with the AutoCAD system, and Claudio Venegas for support. We express special appreciation to our contacts in Chile, the crew of the *Chonos*, staff members of Fantastico Sur Birding and Nature, and government officials of the Ministerio de Economia, Fomento y reconstrucción, Republica de Chile for granting permission to work on Isla Noir. We thank the crew and staff of the *M/S Nordnorge* for close approaches to Terhalten. Our gratitude is also expressed to Clinton Nagy, Edward Maruska, and Greg Hanson for their continued support and participation in this project.

LITERATURE CITED

Araya, B. and G. Millie. 1986. Guia de campo de las aves de Chile. Editorial Universitaria, Santiago de Chile.

Barlow, K. E., I. L. Boyd, J. P. Croxall, K. Reid, I. J. Staniland, and A. S. Brierley. 2002. Are penguins and seals in competition for Antarctic krill at South Georgia? Marine Biology 140:205–213.

Bingham, M. and E. Mejias. 1999. Penguins of the Magellan Region, Scientia Marina 63: Supplement 1:485–493.

BirdLife International 2007a. Species factsheet: *Eudyptes chrysocome*. http://www.birdlife.org (accessed 7 June 2007).

BirdLife International 2007b. Species factsheet: *Eudyptes chrysolophus*. http://www.birdlife.org (accessed 7 June 2007).

Bogaert, P., J. Delincé, and S. Kay. 2005. Assessing the error of polygonal area measurements: a general formulation with applications to agriculture. Measurement Science and Technology 16:1170–1178.

CCAMLR. 1999. Commission for the Conservation of Antarctic Marine Living Resources. CCAMLR Ecosystem Monitoring Program. Standard Method Publication, Tasmania, Australia.

Clark, G. 1988. The Totorore voyage. Century Hutchinson Publisher, Aukland, New Zealand.

Clausen, A. P. and N. Huin. 2003. Status and numerical trends of King, Gentoo, and Rockhopper penguins breeding in the Falkland Islands. Waterbirds 25:389–402.

Crawford, R. J. M., J. Cooper, and B. M. Dyer. 2003. Population of the Macaroni Penguin *Eudyptes chrysolophus* at Marion Island, 1994/95–2002/03, with information on breeding and diet. African Journal of Marine Science 23:475–586.

Crawford, R. J. M., B. M. Dyer, J. Cooper, and L. G. Underhill. 2006. Breeding numbers and success of *Eudyptes* penguins on Marion Island, and

the influence of mass and time of arrival of adults. CCAMLR Science 13:175–190.

Downes, M. C., E. H. M. Ealey, A. M. Gwynn, and P. S. Young. 1959. The birds of Heard Island. Australian National Antarctic Resource Expeditions Report Series B1.

Ellis, C. E. 2005. Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. Plant Ecology 181:227–241.

Ellis, S., J. P. Croxall, and J. Cooper. 1998. Penguin conservation and assessment plan. Apple Valley: IUCN/SSC Conservation Breeding Specialist Group (1996 CAMP Report). Cape Town, South Africa.

Kirkwood, R., K. Lawton, C. Moreno, J. Valencia, R. Schlatter, and G. Robertson. 2007. Estimates of Southern Rockhopper and Macaroni penguin numbers at the Ildefonso and Diego Ramirex Archipelagos, Chile, using quadrat and distance-sampling techniques. Waterbirds 30:259–267.

Krebs, C. J. 1999. Ecological methodology. Second Edition. Addison-Wesley Educational Publication, Menlo Park, California, USA.

Krebs, C. J. 2002. Ecological methodology. Second Edition Software. Department of Zoology, University of British Columbia, Vancouver, Canada.

Oehler, D. A., W. R. Fry, L. A. Weakley, and M. Marin. 2007. Rockhopper and Macaroni penguin colonies absent from Isla Recalada, Chile. Wilson Journal of Ornithology 119:502–506.

Pütz, K., A. P. Clausen, N. Huin, and J. P. Croxall. 2003. Re-evaluation of historical Rockhopper Penguin population data in the Falkland Islands. Waterbirds 26:169–175.

Reilly, P. 1994. Penguins of the world. Oxford University Press, South Melbourne, Australia.

Schiavini, A. C. M. 2000. Staten Island, Tierra del Fuego: the largest breeding ground for Southern Rockhopper Penguins? Waterbirds 23:286–291.

Soto, N. 1990. Proyecto de protección y manejo de las colonias de pingüinos presentes en isla Rupert e isla Recalada, Reserva Nacional Alacalufes. Informe de temporada 1989–1990. CONAF-XII Region, Punta Arenas, Chile.

Thompson, K. R. 1993. Falkland Islands Seabird Monitoring Programme summary of results. Falklands Conservation Report SMP/3. Stanley, Falkland Islands.

Venegas, C. 1984. Estado de las poblaciones de Pinguino de Penacho Amarillo y Macaroni en la Isla Noir, Chile. Informe Instituto de la Patagonia 33.

Venegas, C. 1991. Estudio de cuantificacion poblacional de pinguinos crestados en Isla Recalada. Informe Instituto de la Patagonia 55.

Venegas, C. 1998. Pinguinos crestados (*Eudyptes chrysocome* Forster 1781, *E. chrysolophus* Brant 1837) y de Magallanes (*Spheniscus megellanicus* Forster 1781) en isla Noir, Chile. Anales del Instituto de la Patagonia 26:59–67.

Venegas, C. and N. Soto. 1992. Estudio de pingüinos eudyptidos en isla Recalada, R. N. Alacalufes, Chile. Informe Convernio UMAG-CONAF, Punta Arenas, Chile.

Wallace, G. E. 1991. Noteworthy bird records from southernmost Chile. Condor 93:175–176.

Woehler, E. J. 1993. The distribution and abundance of Antarctic and subantarctic penguins. SCAR, Cambridge, United Kingdom.

Woehler, E. J. and J. P. Croxall. 1997. The status and trends of Antarctic and subantarctic seabirds. Marine Ornithology 25:43–66.

The Wilson Journal of Ornithology 120(3):582–593, 2008

NEST HABITAT SELECTION OF WHITE-WINGED SCOTERS ON YUKON FLATS, ALASKA

DAVID E. SAFINE[1,2,3] AND MARK S. LINDBERG[1]

ABSTRACT.—Breeding bird surveys indicate a long-term decline in numbers of scoters (*Melanitta* spp.) breeding in North America. Little is known about the breeding habitat and reproductive life history of White-winged Scoters (*M. fusca*) in their primary breeding areas in the boreal forest of Alaska and northern Canada. We characterized selection of nest habitats and attributes within those habitats by measuring variables at nests and random sites on the Yukon Flats National Wildlife Refuge, Alaska. White-winged Scoters avoided nesting in meadows, but nested in scrub or forested habitat types in proportion to their availability ($\chi^2_5 = 9.7$, $P = 0.08$). Nests of radio-marked females were farther from water and edge (+210 ± 43 and +10 ± 4 m, respectively), and in slightly thicker cover (+6 ± 4%) than nests located without aid of radio transmitters. Females selected sites with more variable and abundant overhead and lateral cover, and sites closer to edge and water than random sites. The results imply nearly random use of scrub and forested habitat types within the study area, but selective use of attributes within those habitat types. This generalist approach to nest site selection at a larger scale may be an adaptive response to reduce detection by nest predators. Nests located without use of radio-marked females may not be representative of the population of nests at a study site. White-winged Scoters often selected nest sites with dense cover far from water, which may increase nest survival. However, concealed sites are difficult for heavy-bodied birds to escape and females may be trading productivity against their own mortality. *Received 3 November 2006. Accepted 26 December 2007.*

White-winged Scoters (*Melanitta fusca*) breed from the Canadian prairies north and west through the boreal forest of Canada into interior Alaska (Bellrose 1980). The majority of the 884,000 scoters surveyed in North America breed in the northern boreal forest of Canada and Alaska (Canadian Wildlife Service Waterfowl Committee 2006). The Yukon Flats National Wildlife Refuge (hereafter Yukon Flats) in eastern interior Alaska has one of the densest populations of breeding White-winged Scoters in North America (Bellrose 1980). North American surveys of scoters (Black [*Melanitta nigra*], Surf [*M. perspicillata*], and White-winged scoters) indicate breeding populations have declined 1.1% per year in areas surveyed since 1961 (Canadian Wildlife Service Waterfowl Committee 2006). The Alaska population of breeding scoters has been stable or gradually declining (−0.4%/year, $P > 0.05$), whereas scoter populations in the western Boreal Canada and Canadian Prairie strata have been declining more rapidly (−1.3 and −4.6%/year, respectively) since 1961 (Canadian Wildlife Service Waterfowl Committee 2006).

Studies of breeding White-winged Scoters (hereafter scoter) in North America are almost exclusively limited to island nesting populations in the prairie-parkland of Saskatchewan and Alberta (Brown and Brown 1981, Kehoe 1989, Traylor et al. 2004). However, the landscape and plant communities of prairie parkland, grasslands and agricultural fields interspersed with groves of deciduous trees are quite different from the northern boreal forest, which is dominated by coniferous trees and includes a much lesser extent of grasslands (Johnson et al. 1995). Nest sites in the boreal forest may differ from those in the southern portion of the breeding range where less forested area is available. Characterizing the breeding habitat of White-winged Scoters in Alaska and Canada is an information need identified by the Sea Duck Joint Venture Management Board (2001). Oil and gas development has been proposed on both the Mackenzie Delta (Haszard 2001) and Yukon Flats (USDI 2005), both important scoter breeding areas. Describing patterns of nest habitat use in the northern boreal forest will provide baseline information important to managers developing future conservation plans (Haszard 2001, 2004).

Nest site selection is also important in un-

[1] University of Alaska Fairbanks, Department of Biology and Wildlife, and Institute of Arctic Biology, Fairbanks, AK 99775, USA.

[2] Current address: Alaska SeaLife Center, P. O. Box 1329, Seward, AK 99664, USA.

[3] Corresponding author;
e-mail: david_safine@alaskasealife.org

derstanding population dynamics because nest location can affect nest (Martin 1993b, Filliater et al. 1994, Gloutney and Clark 1997) and female survival; thus, individual females may have trade-offs between selecting sites that maximize nest survival while minimizing their own mortality risk (Hoekman et al. 2002a). This trade-off may have population-level effects because both nest and female survival are relatively important factors affecting population growth (Hoekman et al. 2002b).

Nest site characteristics that can affect survival include habitat type and vegetation layers (Crabtree et al. 1989; Martin 1993a, 1995); nests on islands often have higher survival than those on the mainland (Lokemoen and Woodward 1992, Walker et al. 2005). Distance of nests from water and edge (Clark and Shutler 1999, Traylor et al. 2004), vegetative heterogeneity (Crabtree et al. 1989), and cover at nest sites (Badyaev 1995, Clark and Shutler 1999, Traylor et al. 2004) can also affect nest survival. White-winged Scoters in previous studies have been observed nesting far from water in dense and often thorny shrubs, and on islands (Brown and Brown 1981, Brown and Fredrickson 1989, Traylor et al. 2004); following the general patterns of nest site selection in waterfowl. We believed that scoters in the boreal forest would select similar sites to those in prairie-parkland and predicted we would observe greater vegetative cover and variability, greater distances to water and edge, and more scrub plant communities at scoter nests than at random sites.

Quantifying habitat differences between nests and random sites has revealed patterns of habitat use that have improved survival of nests and females over evolutionary time (Clark and Shutler 1999). Additionally, because selection can be quantified hierarchically (Johnson 1980), we believed it would be useful to investigate differences between nests and random sites at multiple scales. The objectives of this study were to examine patterns of site use for nesting White-winged Scoters in the northern boreal forest at two spatial scales: (1) comparison of used and available habitat types, "third-order" selection or the selection of specific habitat components within a home range (Johnson 1980); and (2) comparison of the site attributes of nests and random points, "fourth-order" selection or a more specific level of use within that habitat type (Johnson 1980).

METHODS

Study Area.—We collected data during the breeding season (May–Aug) from 2002 to 2004 on the Yukon Flats, ~170 km north of Fairbanks, Alaska (Fig. 1). The Yukon Flats includes ~3.5 million ha along the Yukon River floodplain in east-central Alaska and encompasses the largest interior wetland basin in Alaska (Heglund 1988). This basin is an area of major importance under the North American Waterfowl Management Plan (USDI 1986). We studied breeding ecology at the Scoter Lake complex (66° 14′ N, 146° 23′ W) in south central Yukon Flats. This area includes a series of relatively large (~1.5 km long) inter-connected lakes and boreal forest (taiga) habitat covering ~4,400 ha. The forest habitats are dominated by: white and black spruce (*Picea glauca* and *P. mariana*, respectively), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Willow (*Salix* spp.), shrub birch (*Betula glandulosa*), alder (*Alnus* spp.), and immature or stunted tree species dominate the scrub habitats. Grasses (e.g., *Calamagrostis* spp. and *Hordeum* spp.), sedges (*Carex* spp.), and emergent plants (e.g., *Typha* spp., *Scirpus* spp., and *Nuphar* spp.) predominate in herbaceous habitats.

Nest Searching.—White-winged Scoters often nest far from water or in thick cover (Brown and Brown 1981) and we used two different methods to locate nests: foot searches with the aid of a dog (Kehoe 1989) and tracking of females marked with radio transmitters prior to nesting. We captured scoters by driving them into floating mist nets (Kaiser et al. 1995), modified for duck capture, from 31 May to 13 June 2002–2004. We outfitted females with prong and suture radio transmitters (Model A4430, 9 g, Advanced Telemetry Systems, Isanti, MN, USA; Mauser and Jarvis 1991, Rotella et al. 1993) modified with glue. Each female was tracked daily from the ground and once or twice weekly from an airplane until we either found her nest or confirmed her as a failed or non-breeder. We attempted to ascertain the status of females located on water (paired or not paired) without

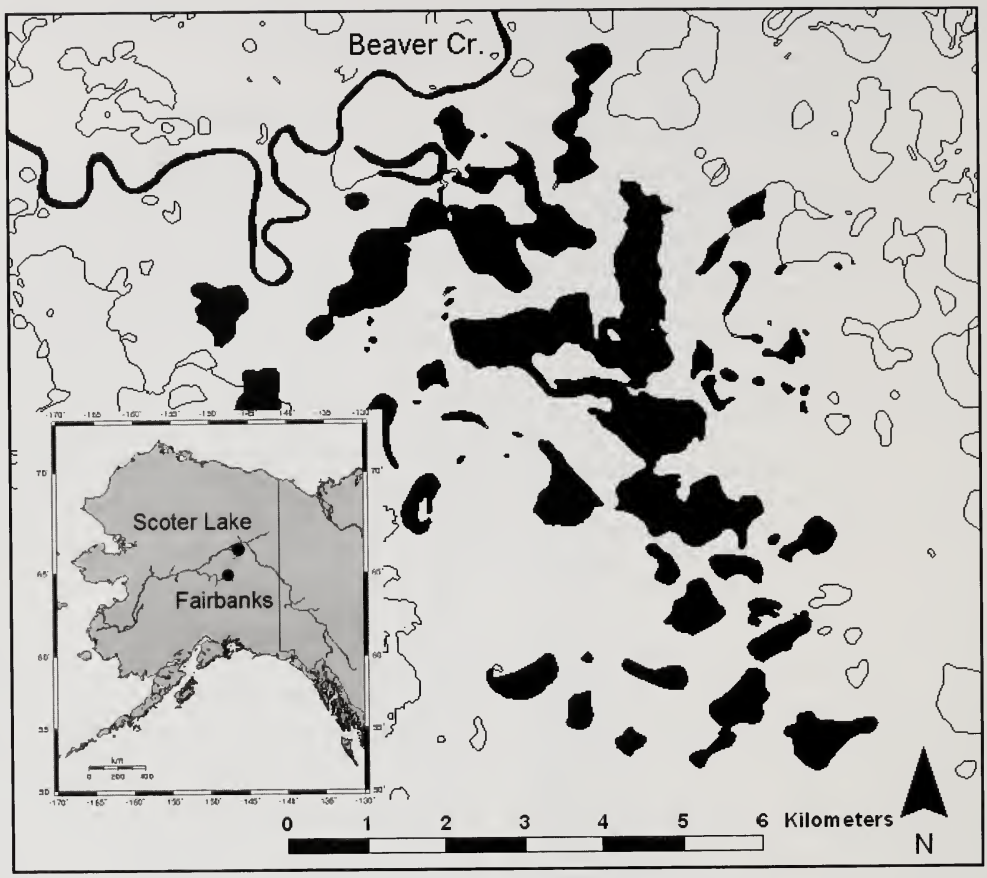


FIG. 1. Scoter Lake complex, south central Yukon Flats National Wildlife Refuge, Alaska. Darkened areas indicate water in the study area, 2002–2004.

flushing them. We attempted to find nests of females on land without flushing them.

We searched lakeshores, islands, peninsulas, bog perimeters, and areas within 600 m of water for nests on foot from 0800 to 1600 hrs ADT from 21 June to 17 July each year. We defined a scoter nest as a depression with either down, eggs, or contour feathers identified as White-winged or Surf scoter. We found nests initiated in the current or previous year and included active, destroyed, and hatched scoter nests in our sample. We were able to include nests initiated in the previous year because typically sufficient feathers and/or egg shells remained in the depression to positively identify the nest. We recorded latitude and longitude data for all nests with a compact Global Positioning System (GPS) unit (± 6 m accuracy).

Nest Habitat.—We entered GPS coordinates of all nests from 2002 to 2004 into a data base and plotted them on ArcView 3.3 (Environmental Systems Research Institute, Redlands, CA, USA) geographic information system program. We used the Animal Movement extension (Hooge and Eichenlaub 2000) to draw a minimum convex polygon for the entire sample of nest sites and generated 80 random locations within this polygon. Random sites were spaced at least 200 m apart with no distance to polygon border restrictions. We excluded random sites in lakes, but visited all sites within 50 m of the mapped lakeshore, as lake levels have changed since U.S. Geological Survey maps were developed in 1956.

We visited all nest and random sites from 28 July to 14 August in 2003 and 2004 to record site characteristics. We recorded (1) habitat type, (2) edge type, (3) distance to edge, (4) distance to water, (5) overhead cover,

and (6) lateral cover at each site. We measured this suite of variables because we predicted they would affect female, nest, and duckling survival and, potentially, the process of site selection. We classified habitat type using the level II categories in the Alaska Vegetation Classification (Heglund 1992, Viereck et al. 1992) defined as the proportion of cover types in a 10-m radius circle centered on the nest or random point. We defined distance to edge as the distance to the nearest change in habitat type (Clark and Shutler 1999, Clark et al. 1999) and edge type as the habitat type present beyond that change or nearest different habitat type (Clark et al. 1999). We measured distance to water (Clark and Shutler 1999, Traylor et al. 2004) as the minimum distance to a body of water sufficiently large to appear on infrared photographs of the area.

We marked additional points 5 m from the nest or random location to better characterize each site. In 2003, we visited nests found in 2002 and 2003, and marked four additional points in the cardinal directions around these nests. In 2004, we visited nests located that year and all random points marking two additional points at random bearings around each site. We reduced additional points (from 4 to 2) in 2004 because of logistical constraints associated with the four-fold increase in number of sites to visit that year.

We recorded overhead and lateral cover only at each of the two (four) outside points (Fig. 2.) We measured overhead cover (Clark and Shutler 1999, Traylor et al. 2004) with a spherical convex crown densiometer placed on the ground and averaged from the four cardinal directions. We measured lateral cover as the average percent obstruction of five white 6.5-cm^2 blocks on a black cardboard square (Clark and Shutler 1999) viewed 2 m from the side at a height of 60 cm taken from the four cardinal directions. Each site was characterized by the average value of overhead and lateral cover measured at the center and outside points. We defined overhead and lateral cover variation as the standard deviation of the three or five measurements of overhead and lateral cover at each site. We sampled additional random sites in the dwarf tree and tall scrub habitats after visiting all random sites, because they were rare. We needed to increase the sample of random sites in the two rare habitat types to be greater than or equal to the number of nests in rare habitat types.

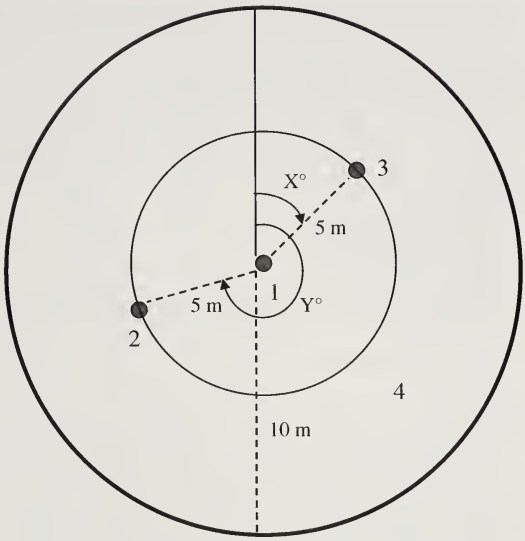


FIG. 2. Sampling protocol for nests and random points. 1 = nest site or GPS coordinates of the random point, 2 and 3 are additional sampling points 5 m from the center, and 4 is the habitat type of the 10-m circle around the center point. X and Y are random bearings for additional points.

Use versus Availability.—We performed all statistical analyses using SAS software (SAS Institute 1999). We used a Chi-square test of homogeneity (PROC FREQ) to test for equal proportions of nests and random sites in each habitat type because availability was estimated from random sites (Marcum and Loftsgaarden 1980, Thomas and Taylor 1990). We performed the analysis with and without habitat types that were commonly available but rarely used (Thomas and Taylor 1990). We also performed a test of homogeneity on the proportion of edge habitat types at both nest and random sites in habitat types used for nesting. We verified that expected frequencies were greater than one and the average expected frequencies were greater than six to assure appropriateness of the Chi-square test (Zar 1999).

Effects of Sampling Design and Nest Searching Method.—We examined differences in mean cover and variation values at nests in 2003 and 2004 (5 and 3 sampling points per site, respectively; PROC TTEST) to ascertain if both protocols provided sufficiently similar results to warrant their combination in the

TABLE 1. Proportion of White-winged Scoter nests and random points in each habitat and edge type with associated cell Chi-square values from the test of homogeneity; Scoter Lake complex, Yukon Flats National Wildlife Refuge, Alaska, 2002–2004.

	Nests			Random sites			Overall	
	n	%	Cell χ^2	*n*	%	Cell χ^2	Total χ^2	*P* value
Habitat type								
Coniferous forest	16	40	0.0	26	43	0.0		
Deciduous forest	2	5	0.1	4	7	0.0		
Mixed forest	13	33	0.1	17	28	0.1		
Dwarf tree scrub	5	13	2.9	1	2	1.9		
Tall scrub	4	10	0.0	6	10	0.0		
Graminoid herbaceous	0	0	2.8	7	12	1.8		
Totals	40	100	5.9	61	100	3.9	9.7	0.08
Edge type								
Coniferous forest	7	18	0.2	7	13	0.2		
Deciduous forest	3	8	0.2	6	11	0.1		
Mixed forest	7	18	0.0	10	19	0.0		
Dwarf tree scrub	4	10	0.9	2	4	0.6		
Tall scrub	4	10	2.0	15	28	1.4		
Graminoid herbaceous	5	13	0.4	4	7	0.3		
Water	9	23	0.1	10	19	0.1		
Totals	39	100	3.8	54	100	2.7	6.5	0.37

analysis. We also investigated differences in nest site characteristics attributable to the search method (radiotelemetry or ground searches with aid of dogs; PROC TTEST) to understand how method used may affect subsequent analyses.

Site Attributes.—We used logistic regression (PROC LOGISTIC) to characterize which habitat features affected selection (Alldredge et al. 1998) within habitat types. Our sampling protocol was consistent with a use-availability study as an approximation to a case-control design, which requires the assumption that use of available sites is rare (Keating and Cherry 2004). We interpreted the results of logistic regression as odds ratios and not resource selection functions as we were making the rare use assumption (Keating and Cherry 2004).

The explanatory variables used in the models were habitat type, distances to edge and water, lateral and overhead cover, and variation of lateral and overhead cover. We included 12 additional random points to increase sample size in rare habitat types to achieve a sample of available sites in approximate proportion to use. We used habitat type to explain variation in the logistic regression models because we sampled in proportion to use, but not to infer selection of habitat types themselves. We investigated correlations among explanatory variables with correlation analysis (PROC CORR) and scatter plots. We chose an *a priori* model set of 41 biologically relevant models and all models with more than two parameters included only additive effects. We used Akaike's Information Criteria (Akaike 1973) adjusted for small sample size (AIC_c; Burnham and Anderson 1998) for model selection. We tested goodness-of-fit to the logistic model with the Hosmer and Lemeshow (1989) statistic. Values reported are means ± SE.

RESULTS

Use versus Availability.—We visited random sites that were on land ($n = 61$) in all six terrestrial habitat types: coniferous, deciduous, and mixed forest; dwarf tree and tall scrub; and graminoid herbaceous. We located scoter nests ($n = 3$, 17, and 20 [one of which was a Surf Scoter] in 2002, 2003, and 2004, respectively) in five of the six terrestrial habitat types on the study area; only graminoid herbaceous habitat was unused (Table 1). The edge habitat at nests and random points included all six terrestrial habitats plus water (Table 1). Nests ($n = 40$) and random sites (n

TABLE 2. Site attributes of White-winged Scoter nests and random points; Scoter Lake complex, Yukon Flats National Wildlife Refuge, Alaska, 2002–2004.

Parameter[a]	Nests (n = 39)		Random points (n = 62)			
	Mean	SE	Mean	SE	Difference[b]	SE
Distance to edge	12.3	2.0	29.2	5.3	*−16.9	6.9
Distance to water	144.3	26.1	240.6	23.3	*−96.3	35.9
Overhead cover	78.9	1.8	73.8	1.9	5.1	2.8
Overhead cover variation	12.1	1.4	11.0	1.0	1.1	1.7
Lateral cover	55.7	2.4	45.1	2.5	*10.6	3.7
Lateral cover variation	16.3	1.2	13.9	1.0	2.4	1.6

[a] Distance in meters, cover as percent obstruction, and variation in cover as standard deviation of percent obstruction.
[b] * P-value <0.01.

= 54 without graminoid sites, n = 61 with graminoid points) were present in the same proportions among habitat types (Table 1) whether or not we included the graminoid herbaceous habitat type that was available but unused (without graminoid; $\chi^2_4 = 4.7$, $P = 0.32$). The proportion of edge type at nests (n = 39) and random sites (n = 54) was equal among the seven edge habitat types (Table 1).

Effects of Sampling Design and Nest Searching Method.—We located 40 nests of which six were initiated the year prior to discovery; 15 nests were found by monitoring radio-marked females and 25 nests were found while conducting ground searches with a dog. There were minimal differences in mean overhead cover (2 ± 4%) and lateral cover (7 ± 5%) between nests with three sampling points (n = 19) and five sampling points (n = 20). Mean variation in overhead (0 ± 3%) and variation in lateral cover (−2 ± 2%) did not differ between nests with three sampling points (n = 19) and five sampling points (n = 20). Sampling design differences between years did not affect parameter estimates in the regression model and combining sampling designs was warranted. However, mean distances to water and edge were greater at nests found using telemetry (+210 ± 43 and +10 ± 4 m, respectively) than at nests found with ground searches; there was some evidence that overhead cover was also greater (+6 ± 4%).

Site Attributes.—We included random points (n = 50) in the five habitat types that scoters used for nesting: coniferous, deciduous, and mixed forest, dwarf tree and tall scrub, and additional points in dwarf tree and tall scrub (n = 9 and 3, respectively). Four random points had water within 5 m and were not included in the analysis because water restricted the directions available to place the additional points. Nests were closer to edge and water, and had denser and more variable cover than random points (Table 2).

The best approximating model in the logistic regression was that site use depends on the additive relationship of all measured variables (distance to edge and water, overhead and lateral cover, variation in both overhead and lateral cover, and habitat type simplified into 2 categories, forest or scrub). Five other models were within seven AIC_c units, but none was within two AIC_c units of the most parsimonious model (Table 3). The top three models were similar and all included distance effects (edge and water) and cover effects (overhead and lateral). The top model included habitat and variation in cover effects, whereas the next best model added only variation in cover effects. The Hosmer and Lemeshow goodness-of-fit test indicated the most parameterized model fit the logistic model ($\chi^2_8 = 4.6$, $P = 0.80$). Probabilities predicted by the top model were 85% concordant and 15% discordant with the observed data. Coefficient and odds ratio estimates from the top model (Tables 4, 5) indicated all variables explain variation in the data with the exception of variation in lateral cover. The odds of site use decreased at sites farther from water and edge; however, odds of site use increased with greater lateral and overhead cover as well as variation in lateral and overhead cover. In the top model, distance to water changed the odds ratio of use much slower than distance to edge (Fig. 3); the same relationship was true for the odds ratios of lateral and overhead cover (Fig.

TABLE 3. Model selection from logistic regression of White-winged Scoter nest site attributes and location (nest or random point); Scoter Lake complex, Yukon Flats National Wildlife Refuge, Alaska, 2002–2004. Models are shown with sources of variation in location; plus symbols indicate additive relationships among parameters. Number of parameters (k), -2*log likelihood ($-2log(l)$), the difference in Akaike's information criterion adjusted for small sample size from the best approximating model (ΔAIC_c), and the coefficient of determination (R^2) are included with results from models with $\Delta AIC_c \leq 7$.

Model[a]	k	$-2\ log(l)$	ΔAIC_c	R^2
De + Dw + Oc + Ocv + Lc + Lcv + Hab2	8	94.1	0.0	0.33
De + Dw + Oc + Ocv + Lc + Lcv	7	99.2	2.7	0.30
De + Dw + Oc + Lc	5	105.6	4.6	0.25
De + Dw + Oc + Ocv + Lc + Lcv + Hab5	11	92.7	6.0	0.34
De + Dw + Oc	4	110.1	6.9	0.22
De + Dw + Lc	4	110.2	7.0	0.22

[a] Model parameters are distance to edge (De), distance to water (Dw), overhead cover (Oc), overhead cover variation (Ocv), lateral cover (Lc), lateral cover variation (Lcv), coarse level habitat type, two classes (Hab2), and habitat type, five classes (Hab5).

4). Overhead cover variation increased the odds ratio of use ~100 times over its range making its effect size larger than lateral cover, but smaller than overhead cover (Fig. 5).

The only two highly correlated variables were overhead cover and variation in overhead cover ($r = -0.67$, $P < 0.001$). Despite this correlation, the top model (Table 3), which included both overhead cover and variation in overhead cover, fit the data much better than models with one of these parameters missing. The ΔAIC_c for the top model without overhead cover included was 7.1 and the top model without overhead cover variation was 4.5 suggesting these correlated variables reduced the deviance sufficiently to warrant their joint presence in the logistic regression models.

DISCUSSION

Use versus Availability.—Scoters used nesting and edge habitats proportional to their availability. There were no significant differences between use and availability, but there is some biologically meaningful information to be gleaned from this analysis. Of the total Chi-square statistic from the nest habitat analysis, 97% was the result of the deviation of the graminoid and dwarf tree scrub observations from their expected values. This high proportion provided evidence of nesting preference for dwarf tree scrub and avoidance of graminoid habitat. Dwarf tree scrub was rare on the study area as it normally occurred only in a narrow area around lakes, which have been decreasing in size over multiple years, and in bogs. However, 13% of the nest sites occurred in this habitat type. This cover type was likely selected because it provided dense woody cover relatively close to water and edge. Graminoid habitats were not rare on the study area (Table 1), but were not used for nesting. While some nests were in a grami-

TABLE 4. Parameter estimates from logistic regression analysis of White-winged Scoter site use as a function of site characteristics at Scoter Lake complex, Yukon Flats National Wildlife Refuge, Alaska, 2002–2004.

Parameter[a]	Estimate	95% Confidence intervals[b]		Standardized estimate[c]
Intercept	−9.72	−16.48	−3.99	
Distance to edge	−0.04	−0.08	−0.01	−0.81
Scrub habitat	−1.60	−3.15	−0.21	
Distance to water	0.00	−0.01	0.00	−0.43
Overhead cover	0.09	0.03	0.16	0.71
Overhead cover variation	0.13	0.03	0.25	0.59
Lateral cover	0.05	0.01	0.09	0.50
Lateral cover variation	0.01	−0.06	0.08	0.03

[a] Beta parameters from the best approximating model.
[b] Profile likelihood confidence intervals.
[c] Beta parameters standardized with respect to different measurement units of site attributes.

TABLE 5. Odds ratio estimates and 95% profile likelihood confidence intervals from the top model of a logistic regression analysis of White-winged Scoter site use vs. site characteristics at Scoter Lake complex, Yukon Flats National Wildlife Refuge, Alaska, 2002–2004.

Effect	Odds ratio	Confidence interval	
Distance to edge	0.96	0.92	1.00
Habitat type (scrub/forest)	0.20	0.05	0.87
Distance to water	1.00	0.99	1.00
Overhead cover	1.10	1.03	1.17
Overhead cover variation	1.14	1.03	1.27
Lateral cover	1.05	1.01	1.09
Lateral cover variation	1.01	0.94	1.08

noid patch, there were sufficient trees or shrubs in the 10-m circle around the nest to classify the habitat as forest or scrub.

This pattern of little selection among forest and scrub types, and avoidance of graminoid habitat showed the importance of woody cover at or near a nest. Scoters selected woody cover without regard to habitat type in which it occurred. This apparent random use of woody habitat types for nesting may greatly reduce the search efficiency of potential nest predators (Martin 1993b) reducing the probability that any predator can find scoter nests. This generalist pattern of site selection may also make it difficult to develop management strategies to minimize the effects of development activities on nesting scoters.

Effects of Nest Searching Method.—Some of the site characteristics we measured at nests, especially distance to water, varied by search method. We searched some areas more intensively than others, particularly those habitats close to edges, shorelines, and islands. The farther we searched from water, the more area was available to search, and the lower our probability of detecting a nest. Our probability of finding nests also decreased with increasing distance to edge and overhead cover. Therefore, our sample of nests found by ground searches was likely a biased sample of nests on the study area with respect to the site characteristics we measured, whereas we assumed the sample of nests from radio-marked birds would be representative of the population. We

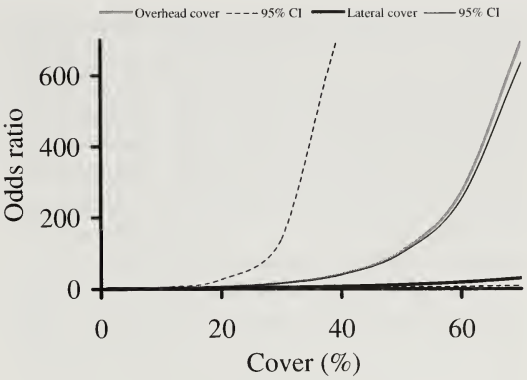


FIG. 4. Effects of overhead and lateral cover on odds ratio of use for breeding White-winged Scoters, Scoter Lake complex, Yukon Flats National Wildlife Refuge, Alaska, 2002–2004.

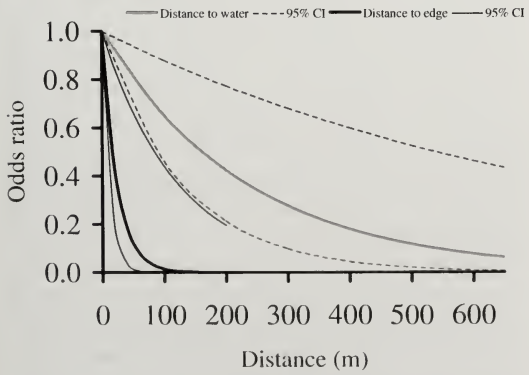


FIG. 3. Effects of distance to water and edge on the odds ratio of use for breeding White-winged Scoters, Scoter Lake complex, Yukon Flats National Wildlife Refuge, Alaska, 2002–2004.

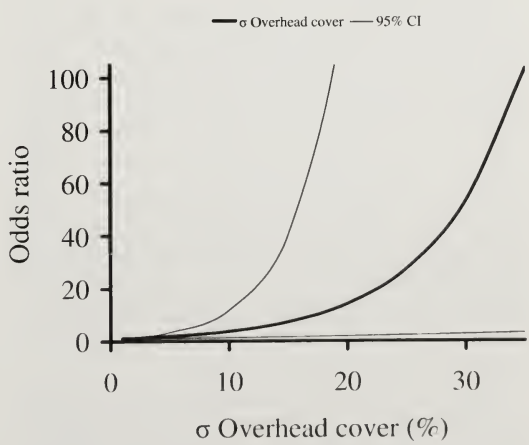


FIG. 5. Effects of overhead cover variation on odds ratio of use for breeding White-winged Scoters, Scoter Lake complex, Yukon Flats National Wildlife Refuge, Alaska, 2002–2004.

targeted and typically captured specific paired females that were near our nets and only a small proportion of our sample was birds that passively flew into the net. Our sample of radio-marked birds is likely representative of the females that can be caught with mist nets and we have no evidence of a capture bias with our targeted mist netting technique because our rate of capture was high.

How could the inclusion of both telemetry and ground search nests in the model affect the results? We may have overestimated the effects of distance to water on site selection, but we could not quantify the magnitude of this bias. However, the distance to water effect is relatively small with all nests included. If only nests located through use of telemetry had been included, it is likely that distance to water would no longer explain variation in site use. The effect of distance to edge would decrease if we included only telemetry nests, but because mean distance to edge only changes +6 m from the mean of all nests (12.3 ± 2.0 m), distance to edge for scoter nests found with telemetry (18.6 ± 4.2 m) would still be lower than the mean value of random sites (29.2 ± 5.3 m); this bias would not change the results dramatically. Similarly for overhead cover, the anticipated change would be small, 4% from the overall mean, and the resulting odds ratio curve would be slightly steeper. Thus, we may be underestimating the effect of overhead cover by including all nests in the analysis.

Site Attributes.—White-winged scoters selected nest sites with more cover and variation in cover, and closer to edge and water than random points at the Scoter Lake complex. Odds of use changed quickly for some parameters in the model over their sampled range, whereas others changed slowly or not at all. Distance to edge and overhead cover were the parameters we measured with the strongest effects on odds of use, while overhead cover variation, lateral cover, and distance to water all had moderate to low (respectively) effects on the odds of use (Figs. 3–5).

The odds of use approached zero when distance to edge values were >120 m; a negative effect. A negative distance to edge effect was also reported for Ring-necked Pheasants (*Phasianus colchicus*) (Clark et al. 1999), and White-winged Scoters nested closer to edge than random sites at Redberry Lake, Saskatchewan (Traylor et al. 2004). In contrast, distance to edge did not differ between nests and unused sites for Wild Turkeys (*Meleagris gallopavo*) (Badyaev 1995), and in five species of dabbling ducks (Clark and Shutler 1999).

Distance to edge for scoters has important implications for nest and female survival. Being farther from edge may improve nest survival (Clark and Shutler 1999) but decrease female survival as they are farther from suitable escape cover often present at edges. If edge habitat is lower or more open than nesting habitat, it may form an opening sufficient for these heavy-bodied birds with "relatively low and slow take-offs" (Brown and Fredrickson 1989: 245) to fly safely from approaching nest predators. Nesting near openings may be extremely important for female survival. Most nests were within 10 m of an opening suitable for escape, but often this opening was too small to be recorded as a unique edge at the scale used in this analysis.

The odds of use slowly decreased as distance to water increased. Nests were on average closer to water than random points (142.7 ± 25.5 m and 231.3 ± 22.8 m, respectively), but sufficient nests were farther from water than random points (18% of the sample) to produce a gradually declining odds ratio. This pattern is similar to that of White-winged Scoters in Saskatchewan, which selected nest sites approximately the same distance from water as random points (~107 m; Traylor et al. 2004). Scoters are known to nest long distances from water (Bellrose 1980, Brown and Brown 1981, this study), but what advantage do scoters receive for nesting far from the safety of lakes? Nesting farther from water may improve nest survival sufficiently to offset potentially negative impacts on females and ducklings during long distance movements to brood rearing habitats. Nesting farther from travel routes of mammalian nest predators (e.g., shorelines and habitat edges) may improve female and nest survival (Brown and Fredrickson 1989, Paton 1994). Nesting scoters appear to be generalists; individual females place their nests varying distances to water and edge in most habitat types, and then seek thick cover at those sites.

Scoters nested in sites with more overhead and lateral cover than random sites, similar to

other waterfowl species (Lokemoen et al. 1984, Clark and Shutler 1999, Traylor et al. 2004). High levels of cover were likely selected by females because they improved nest survival (Badyaev 1995, Clark and Shutler 1999, Traylor et al. 2004). This strategy may reduce detection of the nest, but well-concealed sites are more difficult for these heavy-bodied ducks to exit. Relatively high female mortality (survival probability of 0.80) was observed during the nesting period for White-winged Scoters on this study area as females often nested in heavy cover (Safine 2005). Therefore, females need dense cover to conceal nests and less dense cover nearby for escape, which could be edge habitat or a small opening. The use of escape cover is likely the reason overhead cover variation was an important variable in the model, higher levels of which increased the odds of use. On average, the three points sampled at random sites tended to be more similar to each other, indicating more uniform cover at random sites. Scoters not only selected for high overhead cover, but they chose to place their nests at sites with more heterogeneity in cover.

Scoters selected nest sites from a continuum of available cover densities and distances to water and edge at the Scoter Lake complex. Placement of nests at various levels along this continuum constitutes different solutions to trade-offs in female, nest, and brood survival. Scoters represent waterfowl at one extreme of the cover and distance continuum, often nesting at sites with dense cover far from water (D. E. Safine, pers. obs.). Thus, we would expect scoters to have the highest nest survival and lowest female survival during nesting. Dabbling ducks (Tribe Anatini) are in the center of the continuum and pochards (Tribe Aythyini) are on the other extreme, typically nesting in open sites with floating nests or near the water. We expect pochards to have the lowest nest survival because of the open habitat they select, but high female survival during nesting, as females may easily escape from nests. Despite their poor take-off capabilities and longevity, White-winged Scoters at the Scoter Lake complex often nested at the extreme of the cover and distance continuum. Over the long-term they must experience relatively high nest survival compared to dabbling ducks and pochards; otherwise, this strategy would not persist.

Nesting White-winged Scoters on the Yukon Flats had little selectivity at a larger scale (for specific habitat types) other than avoidance of graminoid meadows. However, scoters appear to be selective at a smaller scale (specific sites within those habitats). This lack of selectivity at a larger scale may improve nest survival over other more selective duck species as predators cannot focus search efforts on scoter nests.

ACKNOWLEDGMENTS

This project was made possible through financial support from the U.S. Fish and Wildlife Service, Yukon Flats National Wildlife Refuge; University of Alaska Fairbanks, Department of Biology and Wildlife and Institute of Arctic Biology; the Jay Hammond Scholarship Fund; and the Sea Duck Joint Venture. We extend our gratitude to our field assistants for their hard work despite the difficult field conditions: K. H. Martin, H. F. Knudsen, J. E. Minerva, S. J. Dufford, James Akaran, C. M. Harwood, Jessica Mensik, A. J. Leppold, K. A. Sesser, J. G. Carlson, Johann Walker, Casey Quitmeyer, S. L. Freeman, L. L. Kennedy, C. S. Van Stratt, M. R. Bertram, B. D. Whitehill, E. T. Heuer, S. W. Wang, Emma, and Minto. We thank the staff of Yukon Flats National Wildlife Refuge for their enthusiastic project support and providing extensive field equipment, and extend a special thanks to M. R. Bertram for assuring we had the equipment, personnel, and logistical support to achieve our goals, and M. T. Vivion for countless hours of aircraft logistical support and radio-telemetry flights. We thank D. H. Rosenberg and M. J. Petrula, Alaska Department of Fish and Game, and P. L. Flint and J. L. Schamber, U.S. Geological Survey, for use of bird capture equipment. We appreciate the GIS assistance provided by S. J. Dufford and N. J. Pamperin. J. W. Hupp, C. P. H. Mulder, E. C. Murphy, and two anonymous referees provided valuable reviews of previous versions of this manuscript.

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* International symposium on information theory (B. N. Petran and F. Csaki, Editors). Akademiai Kiado, Budapest, Hungary.

Alldredge, J. R., D. L. Thomas, and L. L. McDonald. 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3:237–253.

Badyaev, A. V. 1995. Nesting habitat and nesting success of eastern Wild Turkeys in the Arkansas Ozark Highlands. Condor 97:221–232.

Bellrose, F. C. 1980. Ducks, geese and swans of North America. Third Edition. Stackpole Books, Harrisburg, Pennsylvania, USA.

Brown, P. W. and M. A. Brown. 1981. Nesting biology of the White-winged Scoter. Journal of Wildlife Management 45:38–45.

Brown, P. W. and L. H. Fredrickson. 1989. White-winged Scoter populations and nesting at Redberry Lake, Saskatchewan. Canadian Field-Naturalist 103:240–247.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Canadian Wildlife Service Waterfowl Committee. 2006. Population status of migratory game birds in Canada: November 2006. Migratory Birds Regulatory Report 19. Canadian Wildlife Service, Ottawa, Ontario, Canada.

Clark, R. G. and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks. Ecology 80:272–287.

Clark, W. R., R. A. Schmitz, and T. R. Bogenschutz. 1999. Site selection and nest success of Ring-necked Pheasants as a function of location in Iowa landscapes. Journal of Wildlife Management 63: 976–989.

Crabtree, R. L., L. S. Broome, and M. L. Wolfe. 1989. Effects of habitat characteristics on Gadwall nest predation and nest-site selection. Journal of Wildlife Management 53:129–137.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96:761–768.

Gloutney, M. L. and R. G. Clark. 1997. Nest-site selection by Mallards and Blue-winged Teal in relation to microclimate. Auk 114:381–395.

Haszard, S. L. 2001. Habitat requirements of White-winged and Surf scoters in the Mackenzie Delta region, Northwest Territories. Arctic 54:472–473.

Haszard, S. L. 2004. Habitat use by White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*Melanitta perspicillata*) in the Mackenzie Delta region, Northwest Territories. Thesis. University of Saskatchewan, Saskatoon, Canada.

Heglund, P. J. 1988. Relationship between waterbird use and limnological characteristics of wetlands on the Yukon Flats National Wildlife Refuge, Alaska. Thesis. University of Missouri, Columbia, USA.

Heglund, P. J. 1992. Patterns of wetland use among aquatic birds in the interior boreal forest region of Alaska. Dissertation. University of Missouri, Columbia, USA.

Hoekman, S. T., I. J. Ball, and T. F. Fondell. 2002a. Grassland birds orient nests relative to nearby vegetation. Wilson Bulletin 114:450–456.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002b. Sensitivity analyses of the life cycle of midcontinental Mallards. Journal of Wildlife Management 66:883–900.

Hooge, P. N. and B. Eichenlaub. 2000. Animal movement extension to Arcview. Version 2.0. USGS, Alaska Science Center-Biological Science Office, Anchorage, USA.

Hosmer, D. W. and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, J. D., L. Kershaw, A. MacKinnon, and J. Pojar. 1995. Plants of the western boreal forest and aspen parkland. First Edition. Lone Pine Publishing. Renton, Washington, USA.

Kaiser, G. W., A. E. Derocher, S. Crawford, M. J. Gill, and I. A. Manley. 1995. A capture technique for Marbled Murrelets in coastal inlets. Journal of Field Ornithology 66:321–333.

Keating, K. A. and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774–789.

Kehoe, F. P. 1989. The adaptive significance of creching behaviour in the White-winged Scoter *Melanitta fusca deglandi*. Canadian Journal of Zoology 67:406–411.

Lokemoen, J. T. and R. O. Woodward. 1992. Nesting waterfowl and waterbirds on natural islands in the Dakotas and Montana. Wildlife Society Bulletin 20:163–171.

Lokemoen, J. T., H. F. Duebbert, and D. E. Sharp. 1984. Nest spacing, habitat selection, and behavior of waterfowl on Miller Lake Island, North Dakota. Journal of Wildlife Management 48:309–321.

Marcum, C. L. and D. O. Loftsgaarden. 1980. A nonmapping technique for studying habitat preferences. Journal of Wildlife Management 44:963–968.

Martin, T. E. 1993a. Nest predation among vegetation layers and habitat types: revisiting the dogmas. American Naturalist 141:897–913.

Martin, T. E. 1993b. Nest predation and nest sites. Bioscience 43:523–532.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101–127.

Mauser, D. M. and R. L. Jarvis. 1991. Attaching radio transmitters to 1-day-old Mallard ducklings. Journal of Wildlife Management 55:488–491.

Paton, P. W. C. 1994. The effects of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17–26.

Rotella, J. J., D. W. Howerter, T. P. Sankowski, and J. H. Devries. 1993. Nesting effort by wild Mallards with 3 types of transmitters. Journal of Wildlife Management 57:690–695.

Safine, D. E. 2005. Breeding ecology of White-winged Scoters on the Yukon Flats, Alaska. Thesis. University of Alaska, Fairbanks, USA.

SAS Institute. 1999. SAS. Version 8.0. SAS Institute Inc., Cary, North Carolina, USA.

Sea Duck Joint Venture Management Board. 2001. Sea Duck Joint Venture Strategic Plan: 2001–2006. Unpublished Report. Sea Duck Joint Venture Continental Technical Team, USDI, Fish and Wildlife Service, Anchorage, Alaska, USA; Canadian Wildlife Service, Sackville, New Brunswick, Canada.

Thomas, D. L. and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322–330.

Traylor, J. J., R. T. Alisauskas, and F. P. Kehoe. 2004. Nesting ecology of White-winged Scoters *Melanitta fusca deglandi* at Redberry Lake, Saskatchewan. Auk 121:950–962.

U.S. Department of Interior (USDI). 1986. North American waterfowl management plan: a strategy for cooperation. USDI, Fish and Wildlife Service, Washington, D.C., USA.

U.S. Department of Interior (USDI). 2005. Evaluation and review of a proposed land exchange and acquisition of native lands within the Yukon Flats National Wildlife Refuge, Alaska. USDI, Fish and Wildlife Service, Anchorage, Alaska, USA.

Viereck, L. A., C. T. Dyrness, A. R. Batten, and K. J. Wenzlick. 1992. The Alaska vegetation classification. USDA, Forest Service, General Technical Report PNW-GTR-286. Pacific Northwest Research Station, Portland, Oregon, USA.

Walker, J., M. S. Lindberg, M. C. MacCluskie, M. J. Petrula, and J. S. Sedinger. 2005. Nest survival of scaup and other ducks in the boreal forest of Alaska. Journal of Wildlife Management 69: 582–591.

Zar, J. H. 1999. Biostatistical analysis. Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Short Communications

The Wilson Journal of Ornithology 120(3):594–599, 2008

Use of Legs and Feet for Control by Scoters during Aerial Courtship

William J. Wilson[1]

ABSTRACT.—Scoters (*Melanitta* spp.) exhibit extraordinary maneuvers during courtship flight, attitudes which are not commonly seen in flight. Scoters drop their legs and spread webbed feet during these maneuvers. There appears to be a correlation between how the feet of scoters meet the airflow and the maneuver in progress. *Received 25 April 2007. Accepted 5 August 2007.*

Block Island Sound, New York/Rhode Island, USA supports large populations of scoters (*Melanitta* spp.) in late winter and early spring. Groups of each species of scoter form courting parties at this time, comprised of a single hen with an entourage of drakes (Gunn 1927, McKinney 1959). Airborne courting parties in late winter exhibit uncommon flight patterns which include steep climbs (Wilson 1980), abrupt turns, and slow fluttering flight. Often during these maneuvers the birds drop their legs so the spread webbed feet can engage the airflow.

I spent weekends through the 1970s photographing scoters during late winter and early spring near Montauk, New York (41° 03′ N, 72° 00′ W) at the eastern end of Long Island, where the Montauk Lighthouse faces the southern terminus of Block Island Sound and the adjoining Atlantic Ocean. The objective of this paper is to describe how the feet of scoters are used in aerial maneuvers during this early courtship period. Six figures are discussed that support these descriptions.

OBSERVATIONS

A Surf Scoter (*Melanitta perspicillata*) courting party transitions from straight ahead flight to an abrupt turn because the lone hen (Fig. 1, arrow 1) departs the formation. In this sequence the highest drake brakes with both feet prior to turning. Just below him a drake (Fig. 1, arrow 2) rotates his extended right leg in a counter-clockwise direction about the roll axis to a position that, rather than below, is beside his body (Fig. 2). His open (braking) foot, being perpendicular to the incident airflow, is subject to only the force of drag. This force is proportional to the square of the airflow velocity (Videler 2005:7) and, acting in the same direction as airflow and coupling to the bird's body by the extended leg, produces clockwise rotational force about the yaw axis that is part of the mechanics of the turn.

Similarly, the feet of at least two of the descending Black Scoter (*M. nigra*) (Fig. 3B, arrows 1 and 2) are presented to the headwind to produce only drag. The descending courting party is depicted (Fig. 3A) in varied transient attitudes, all with deployed webbed feet. The formation flutters to the water with a yawing motion resembling a falling leaf. Supporting this maneuver is a headwind that, judging from the white-caps on Block Island Sound, is a sea state that appears more rough than moderate, indicating a fresh breeze (Beaufort Scale #5) and wind velocity approximated at 30–39 km/hr. The wings of scoters 1 and 2 are configured in a negative dihedral that minimizes control, while their feet are rotated about their roll axis. They shift centers of force that produce the oscillating yawing motion and the strong headwind enhances this control. The birds' large angle of attack is needed to counteract the resulting rotational force the feet produce about the pitch axis.

In contrast, the feet of a Black Scoter courting party (Fig. 4A) are swept back in execution of an abrupt turn. The hen (Fig. 4A, arrow 1) is initially seen in a large angle of attack and braking prior to following a drake (Fig. 4A, arrow 2) out of formation. This drake is executing a banking turn with his swept back feet astride the spread tail. The feet are held at roughly right angles to each other, rather than parallel, and the surface of the right foot is held vertically. Similarly, the hen (Fig. 4B) is making her turn and also holds her right foot vertically (Fig. 5). In

[1] P. O. Box 2285, Montauk, NY 11954, USA; e-mail: jwwilson@optonline.net

FIG. 1. Members of a Surf Scoter courting party execute an abrupt turn to follow the departing hen (arrow 1). A rarely seen turning technique is exhibited by the drake (arrow 2) with the extended foot.

aviation terminology, is this right foot functioning as a vertical stabilizer or a rudder? It is noteworthy the right foot is outboard of the turn, giving it a greater distance from the center of the turn and, thus, a greater angular velocity.

The side-slipping Black Scoter (Fig. 3B, arrow 3) appears almost totally devoid of pitch control due to the vertical attitude of the wings and tail. Control of pitch normally results from the horizontal movement of the

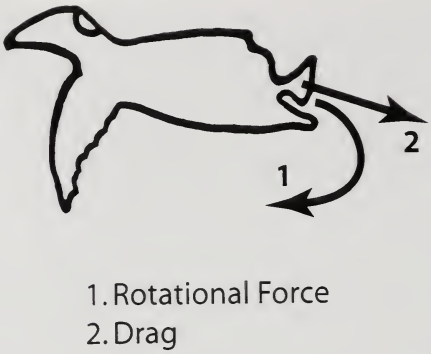


FIG. 2. As the stationary paddle turns a canoe, so too does the force of drag acting on this outstretched foot create rotational force.

wing (Brown 1961:301, Pennycuick 1975:52). The tail's primary use is for pitch (Brown 1961:302). However, the legs and swept back, spread-webbed feet must have significance, if only by default.

A courting party of White-winged Scoter (*M. fusca*, Fig. 6), when heading into the wind, executes a steep climb. A "slight" sea state (Fig. 6) allows approximating the wind speed at 7–19 km/hr, a light to gentle breeze on the Beaufort Scale (#s 2–3). Typically, during this maneuver, the legs deploy the spread webs of the feet astride the tail. The lead drake is at the peak of the climb. The near vertical attitude of the feet in this terminal attitude eliminates increased lift as a reason for their deployment. Their exact function, however, remains unclear.

DISCUSSION

The literature is gradually reflecting that legs and webbed feet of water birds are used for attitude control and maneuver. Brown (1951) suggested it is generally accepted that birds' legs do not contribute to flight, while Barlee (1964:303) believed the feet can produce unbalanced forces. Aymar (1935:32) and Pennycuick (1975:55) both suggest the auk's (*Alcidae*) small tail necessitates control and lift augmentation by the feet. Videler (2005: 27) advocates that, in many species, every aspect of the body is related to flight and, in addition, that legs and feet can alter the center of gravity (Videler 2005:47).

FIG. 3. A descending Black Scoter courting party uses the strong headwind to perform this less than synchronized maneuver. The enlargement (B) better reveals foot positioning and use.

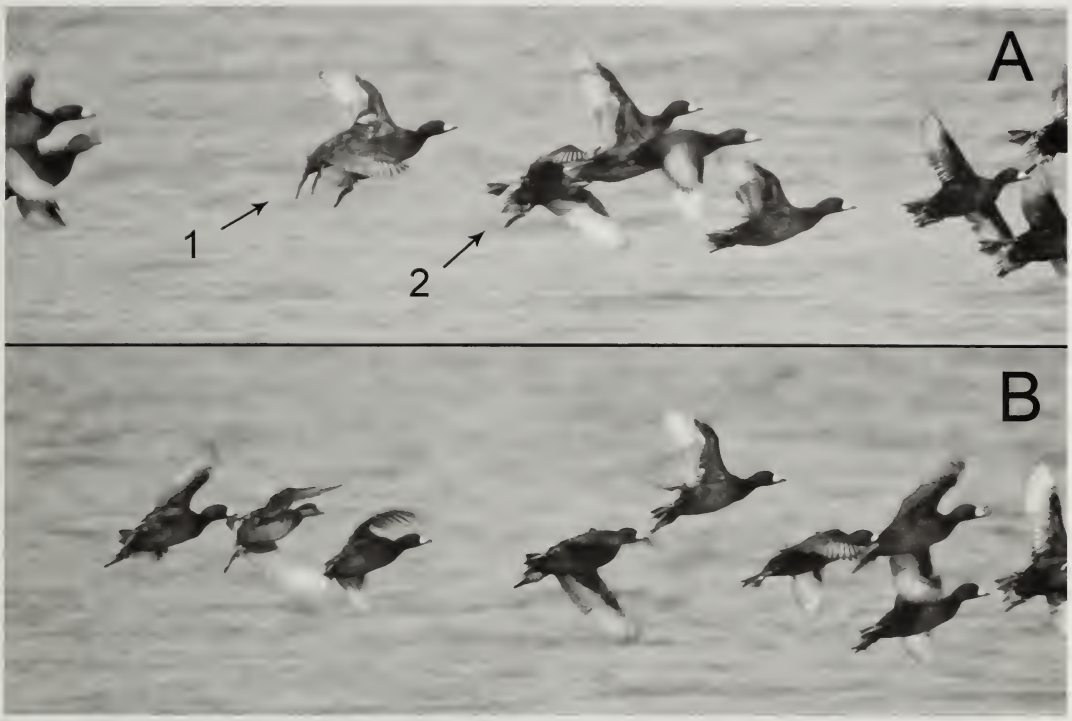


FIG. 4. A two-frame sequence of ~1 sec duration depicts a Black Scoter courting party executing an abrupt turn. Other than the hen in frame A (arrow 1) using her feet to brake, the entire formation has feet swept back.

It is reasonable to assume there is an aerodynamic reason why scoters deploy their legs and spread webbed feet in flight. An extended webbed foot clearly can exert a rotational force about the bird's center of gravity depending on how it interfaces with airflow. This rotational force is exerted upon the airborne body and is either balanced for a trim attitude, or the bird uses the imbalance to change attitude. The reason for the extended foot is elusive in some instances. This is not so for some scoters (Fig. 1, arrow 2; Fig. 3B, arrows 1 and 2). The force of drag acting on the foot with its resulting rotational force is obviously part of an ongoing maneuver; the use of the foot as a control surface is unambiguous.

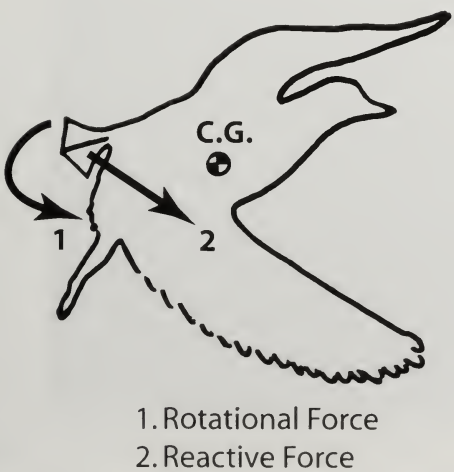


FIG. 5. Is the swept back right foot a vertical stabilizer, or is it a rudder? Any deflection of the airflow by the foot will result in a reactive force that pivots on the center of gravity, resulting in rotational force.

It is only when the foot, from the extended leg, is swept back that conclusions cannot be absolute. The vertically-held right foot (Fig. 4) is part of the maneuver but its function is open to speculation. The higher airflow velocity over the right foot allows it to generate a greater reactive force, suggesting its use as a control surface.

The side-slipping Black Scoter (Fig. 3B, arrow 3) is using his swept back feet. At that instant his only maneuver is descent. That the surfaces of the feet are oriented perpendicular to one another suggests attitude control.

FIG. 6. Gravity surmounts thrust at the peak of a steep climb by White-winged Scoters.

If the lead White-winged Scoter (Fig. 6) was a fixed-wing aircraft, its thrust spent and in a large angle of attack, it would be devoid of control and prone to falling into a spin with possible catastrophic results. However, birds do not spin out. The drake (Fig. 6) maintains a delicate balance prior to the dive that must follow. In pondering how this is done, it is applicable to recall Videler's (2005:27) previously referenced observation, "Not only the wings and the tail but also the head, neck, the body and the hind limbs have features directly related to flight in many species."

ACKNOWLEDGMENTS

I thank P. A. Johnsgard (University of Nebraska–Lincoln), V. A. Tucker (Duke University), and two anonymous reviewers for commenting some thirty years ago on early drafts of this subject. I am grateful for the helpful comments made by the reviewers of this current manuscript. I am indebted to Lindsey Rohrbach (South Fork Natural History Museum) for organizing the digital imagery. Finally, I must acknowledge the literate comments, research, and editing by my wife Janice on whom my dependency is absolute. The original photographs are contained on 35 mm Kodachrome transparencies.

LITERATURE CITED

AYMAR, G. C. 1935. Bird flight. Dodd, Mead and Company, London, United Kingdom.

BARLEE, J. 1964. Flight. Pages 299–307 *in* The new dictionary of birds (A. L. Thomson, Editor). McGraw-Hill, New York, USA.

BROWN, R. H. J. 1951. Flapping flight. Ibis 93:333–359.

BROWN, R. H. J. 1961. Flight. Pages 289–304 *in* Biology and comparative physiology of birds. Volume 2 (A. J. Marshall, Editor). Academic Press, New York, USA.

GUNN, D. 1927. The courtship of the Common Scoter. British Birds 20:193–197.

MCKINNEY, F. 1959. Waterfowl at Cold Bay, Alaska, with notes on the display of the Black Scoter. Wildfowl Trust Annual Report 10:133–140.

PENNYCUICK, C. J. 1975. Mechanics of flight. Pages 1–75 *in* Avian biology. Volume 5 (D. S. Farner and J. R. King, Editors). Academic Press, New York, USA.

VIDELER, J. J. 2005. Avian flight. Oxford University Press, Oxford, United Kingdom.

WILSON, W. J. 1980. Inverted flight of White-winged Scoters during courtship flight. American Birds 34:746–747.

The Wilson Journal of Ornithology 120(3):599–602, 2008

Bill Entanglement in Subcutaneously-anchored Radio Transmitters on Harlequin Ducks

Jeanine Bond[1,3,4] and Daniel Esler[2]

ABSTRACT.—We report two incidences of Harlequin Ducks (*Histrionicus histrionicus*) entangling their bills in subcutaneously-attached anchor transmitters. We suggest caution should be exercised when using these transmitters. *Received 19 May 2007. Accepted 1 November 2007.*

Radio telemetry is an important tool for wildlife research that can reveal valuable information about wild birds that would otherwise be difficult to obtain, such as movements, home ranges, survival, and nest site attributes. However, methods of radio transmitter attachment vary and researchers must choose an attachment that provides adequate retention time, and minimizes detrimental effects. Attachment methods on waterfowl have included backpack harnesses (Dwyer 1972), glue (Perry et al. 1981), tail-mount (Giroux et al. 1990), suture and glue (Wheeler 1991), anchor-suture (Mauser and Jarvis 1991, Pietz et al. 1995), interscapular implants (Korschgen et al. 1996a), and intra-abdominal implants

[1] Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.

[2] Centre for Wildlife Ecology, Simon Fraser University, 5421 Robertson Road, Delta, BC V4K 3N2, Canada.

[3] Current address: 2843 Woodland Drive, Vancouver, BC V5N 3P9, Canada.

[4] Corresponding author;
e-mail: jbond@alumni.sfu.ca

(Korschgen et al. 1996b). Some evaluations of radio transmitters have revealed deleterious effects such as feather wear, lower survival, reduced reproductive effort, behavioral changes, and mass loss (Paquette et al. 1997, Guyn and Clark 1999, Ackerman et al. 2004), whereas other studies have found no significant consequences of transmitters (Houston and Greenwood 1993, Esler et al. 2000, Hepp et al. 2002, Hupp et al. 2006, Iverson et al. 2006). Entanglement is an issue, with potential direct effects on survival, that has been reported for harness transmitters (Keedwell 2001, Duriez et al. 2005), but less frequently with other attachment methods (Conway and Garcia 2005). We report two incidences in which the bills of Harlequin Ducks (*Histrionicus histrionicus*) became entangled with subcutaneously-anchored radio transmitters. This information is important from both ethical and scientific perspectives and informs researchers of potential complications when using these transmitters.

METHODS

We investigated Harlequin Duck breeding and nesting attributes in southern British Columbia during summer in 2003 and 2004. We used transmitters attached by a subcutaneous anchor (Pietz et al. 1995) to adult females to follow them through the breeding season. The transmitters, made by Holohil Systems Ltd. (model RI-2B, Carp, ON, Canada), were a 6-g model with a mortality switch and a life span from 3 to 9 months. They were circular, measured 2 cm in diameter, and had a maximum height of 0.8 cm. We glued stainless steel anchors (Advanced Telemetry Systems, Isanti, MN, USA) to the transmitters opposite the antennae with marine-grade epoxy (Fig. 1).

Each transmitter was attached in the small depression between the scapulae, dorsal to the approximate junction of the cervical and thoracic vertebrae. The feathers were parted using isopropyl alcohol and the site was prepared with Betadine solution (Purdue Frederick Co., Stamford, CT, USA). This attachment site was naturally void of contour feathers and only downy feathers needed to be removed. The transmitter anchor also was cleaned with Betadine solution. The skin was pinched and lifted at the attachment site, and a sterile 18-gauge hypodermic needle was used to puncture a small hole in the skin without contacting the underlying muscle, nerves or blood vessels. No local anesthetic was used because the incision was small and there is believed to be little enervation in this area (Altman 1981, Pietz et al. 1995). The anchor of the transmitter was inserted into the hole, curled end first, and manipulated until the anchor had the head of the arrow pointing forward and resting flat on the bird's back. A quick-drying, veterinary-grade adhesive (Vetbond, 3M, St. Paul, MN, USA) was used around the insertion site to seal the opening, and to glue the top and bottom of the transmitter to the feathers. The females were released immediately after the adhesive dried. These transmitters are normally shed after a period of weeks to months (Iverson et al. 2006).

OBSERVATIONS

We radio-marked 34 female Harlequin Ducks and monitored them from their arrival in breeding areas (late Apr) until the majority of females had departed for wintering areas (early Aug). We had two females (one each year) hook their bills on part of the anchor of the radio transmitter as it began to extrude during the shedding process. The females did not have their bills caught on the transmitter attachment in the same way. The bill of the first female was caught on the curled end of the anchor (Fig. 1), which was slightly open and pierced through the lower mandible of her bill while the looped side of the anchor was still attached subcutaneously to her back. The bill of the second female was caught when her lower mandible became wedged into the loop side of the anchor while the curled end was still attached to her back. The result for both birds was that their heads were held to their backs and, although they were still able to move about, they were likely unable to acquire food during this time. We recaptured both of these females and removed the transmitters. However, if this complication had occurred after we had completed monitoring, these females may have died from starvation or been highly vulnerable to predation.

DISCUSSION

No other study has reported this type of complication from using anchor transmitters.

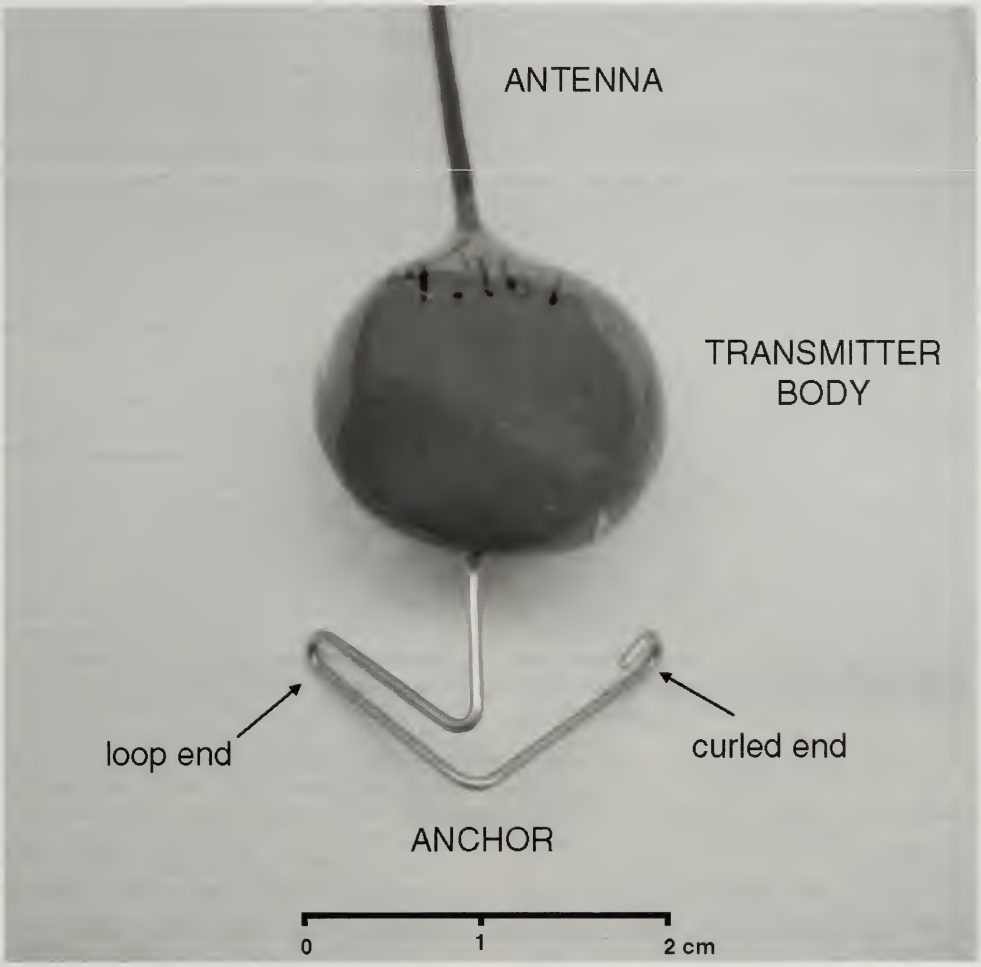


FIG. 1. Illustration of subcutaneously-anchored radio transmitter.

We surmise that Harlequin Ducks are particularly susceptible to this problem because of their small bill size. Pietz et al. (1995) found this type of attachment was retained on some birds for over a year and, in these cases, could lead to feather wear and some abrasion. However, they reported no incidences of the transmitter anchors catching the bills of Mallards (*Anas platyrhynchos*) or Gadwalls (*A. strepera*). Paquette et al. (1997) reported negative effects of anchor transmitters on reproduction and survival of Mallards and suggested this resulted from additional energetic costs associated with increased mass and drag, as well as increased preening. Overall there have been few reports of negative effects from this type of transmitter attachment and many researchers have advocated their use, especially for shorter-term studies (Hepp et al. 2002, Fleskes 2003, Iverson et al. 2006). This attachment method is less surgically invasive than interscapular subcutaneous or intra-abdominal transmitters, and retention times are often appropriate for the battery life of the transmitters. We do not conclude that anchor attachments should be avoided when it is appropriate for the study design, but suggest that potential problems should be considered. Precautionary measures such as using a smaller anchor size, ensuring the curled end is tightly closed, and narrowing the loop end could prevent complications with using this radio attachment method. We advocate that researchers involved in radio telemetry studies make efforts to evaluate, and subsequently report in the primary literature, the effects of

radio transmitters, given their widespread use and potential risks to individual animals and results of studies.

ACKNOWLEDGMENTS

Funding was provided by BC Hydro Bridge Coastal Fish and Wildlife Restoration Program. The Centre for Wildlife Ecology at Simon Fraser University provided logistical support. Chester Alec and Sam Copeland were valuable field technicians, and Sam Iverson, Sunny LeBourdais, Ken Wright, Sean Boyd, and Bobby Vinnie assisted with captures.

LITERATURE CITED

Ackerman, J. T., J. Adams, J. Y. Takekawa, H. R. Carter, D. L. Whitworth, S. H. Newman, R. T. Golightly, and D. L. Orthmeyer. 2004. Effects of radiotransmitters on the reproductive performance of Cassin's Auklets. Wildlife Society Bulletin 32:1229–1241.

Altman, R. B. 1981. General principles of avian surgery. Compendium on Continuing Education for the Practicing Veterinarian 3:177–183.

Conway, C. J. and V. Garcia. 2005. Effects of radiotransmitters on natal recruitment of Burrowing Owls. Journal of Wildlife Management 69:404–408.

Duriez, O., Y. Ferrand, F. Binet, E. Corda, F. Gossmann, and H. Fritz. 2005. Habitat selection of the Eurasian Woodcock in winter in relation to earthworm availability. Biological Conservation 122:479–490.

Dwyer, T. J. 1972. An adjustable radio package for ducks. Bird-Banding 43:282–284.

Esler, D., D. M. Mulcahy, and R. L. Jarvis. 2000. Testing assumptions for unbiased estimation of survival of radio-marked Harlequin Ducks. Journal of Wildlife Management 64:591–598.

Fleskes, J. P. 2003. Effects of backpack radiotags on female Northern Pintails wintering in California. Wildlife Society Bulletin 31:212–219.

Giroux, J.-F., D. V. Bell, S. Percival, and R. W. Summers. 1990. Tail-mounted radio transmitters for waterfowl. Journal of Field Ornithology 61:303–309.

Guyn, K. L. and R. G. Clark. 1999. Decoy trap bias and effects of markers on reproduction of Northern Pintails. Journal of Field Ornithology 70:504–513.

Hepp, G. R., T. H. Folk, and K. M. Hartke. 2002. Effects of subcutaneous transmitters on reproduction, incubation behavior, and annual return rates of female Wood Ducks. Wildlife Society Bulletin 30:1208–1214.

Houston, R. A. and R. J. Greenwood. 1993. Effects of radio transmitters on nesting captive Mallards. Journal of Wildlife Management 57:703–709.

Hupp, J. W., J. M. Pearce, D. M. Mulcahy, and D. A. Miller. 2006. Effects of abdominally implanted radiotransmitters with percutaneous antennas on migration, reproduction, and survival of Canada Geese. Journal of Wildlife Management 70: 812–822.

Iverson, S. A., W. S. Boyd, D. Esler, D. M. Mulcahy, and T. D. Bowman. 2006. Comparison of the effects and performance of four types of radiotransmitters for use with scoters. Wildlife Society Bulletin 34:656–663.

Keedwell, R. 2001. Evaluation of radio transmitters for measuring chick mortality in the Banded Dotterel. Waterbirds 24:217–223.

Korschgen, C. E., K. P. Kenow, A. Gendron-Fitzpatrick, W. L. Green, and F. J. Dein. 1996a. Implanting intra-abdominal radio transmitters with external whip antennas in ducks. Journal of Wildlife Management 60:132–137.

Korschgen, C. E., K. P. Kenow, W. L. Green, M. D. Samuel, and L. Sileo. 1996b. Technique for implanting radio transmitters subcutaneously in day-old ducklings. Journal of Field Ornithology 67: 392–397.

Mauser, D. M. and R. L. Jarvis. 1991. Attaching radio transmitters to 1-day-old Mallard ducklings. Journal of Wildlife Management 55:488–491.

Paquette, G. A., J. H. Devries, R. B. Emery, D. W. Howerter, B. L. Joynt, and T. P. Sankowski. 1997. Effects of transmitters on reproduction and survival of wild Mallards. Journal of Wildlife Management 61:953–961.

Perry, M. C., G. H. Haas, and J. W. Carpenter. 1981. Radio transmitters for Mourning Doves: a comparison of attachment techniques. Journal of Wildlife Management 45:524–527.

Pietz, P. J., D. A. Brandt, G. L. Krapu, and D. A. Buhl. 1995. Modified transmitter attachment method for adult ducks. Journal of Field Ornithology 66:408–417.

Wheeler, W. E. 1991. Suture and glue attachment of radio transmitters on ducks. Journal of Field Ornithology 62:271–278.

The Wilson Journal of Ornithology 120(3):603–606, 2008

Estimate of *Trichomonas gallinae*-induced Mortality in Band-tailed Pigeons, Upper Carmel Valley, California, Winter 2006–2007

Mark R. Stromberg,[1] Walter D. Koenig,[1] Eric L. Walters,[1,3] and John Schweisinger[2]

ABSTRACT.—Band-tailed Pigeons (*Patagioenas fasciata*) wintering at Hastings Reservation in central coastal California during winter 2006–2007 died in large numbers between January and March 2007. Laboratory analysis of carcasses indicated that *Trichomonas gallinae* was responsible for the die-off. During the height of the die-off, a survey of 2.5 km of suitable riparian habitat resulted in 373 pigeon carcasses being found. Based on a subsample of carcasses, mean turnover rate was 2.8 days with a 95% confidence interval of 2–10 days. Extrapolating to suitable habitat over the 52.7-km^2 study area resulted in a conservative estimate of 43,059 dead pigeons, assuming a conservative carcass turnover rate of 10 days. This estimate of mortality is nearly three times the largest trichomoniasis mortality event previously recorded for Band-tailed Pigeons and at least twice the number harvested annually in the United States. Local mortality of pigeons in Monterey County, California may have been several times this estimate based on the presence of considerable similar habitat in the nearby Ventana Wilderness. *Received 27 July 2007. Accepted 14 December 2007.*

Band-tailed Pigeons (*Patagioenas fasciata*) range from Alaska into South America and are seasonally migratory on the Pacific Coast (Keppie and Braun 2000). Most large flocks wintering in central coastal California depart in late April, arriving in British Columbia in May (Keppie and Braun 2000). At Hastings Reservation in the upper Carmel Valley, Monterey County in central coastal California, pigeons are most numerous in winter and fluctuate among years (Davis et al. 1980). From October 2006 to March 2007 large flocks were present feeding largely on coast live oaks (*Quercus agrifolia*) acorns, many of which were still present on a small number of trees throughout the winter. Although a few dead birds are found in most years when pigeons are abundant, unusually high mortality was noted starting in January 2007 with many chronically sick birds observed that were unable to fly and dying.

Band-tailed Pigeons in California and elsewhere are known to have significant mortality due to infections of *Trichomonas gallinae* (Stabler and Braun 1975, 1979; Cole 1999). Our objectives in this paper are to report on the causes of the observed pigeon mortality and present an estimate of the number of pigeons involved.

METHODS

We documented mortality of Band-tailed Pigeons in the vicinity (36° 23′ N, 121° 33′ W) of Hastings Reservation in upper Carmel Valley, California where elevation ranges from 310 to 1,100 m. Pigeons moved widely during the day over a larger area, but roosting at night was usually along riparian corridors. Dead and dying birds were regularly found in these riparian corridors from early January to late March 2007.

Estimating the number of dead pigeons required several steps. First, three observers walked a 2.5-km census transect on Hastings Reservation along Robertson Creek on 7 February 2007 searching the ground on both sides of the creek for fresh pigeon carcasses. Patches of fresh, dry feathers from birds recently depredated, dead birds, and still alive but nonvolant individuals were mapped using handheld GPS units and coordinates were taken for each bird. These data were transformed to distances from a central axis for use with the program DISTANCE® (Thomas et al. 2006) to calculate sample estimates and the effective strip width of the sampling transect.

Second, we estimated the carcass decomposition (turnover) rate by surveying a 1.4-km

[1] Hastings Natural History Reservation and Museum of Vertebrate Zoology, University of California, Berkeley, 38601 East Carmel Valley Road, Carmel Valley, CA 93924, USA.

[2] Turf Images Inc., 177 Webster Street, Monterey, CA 93940, USA.

[3] Corresponding author;
e-mail: ewalters@berkeley.edu

stretch of dirt road paralleling Robertson Creek at the Hastings Reservation over 18 days (8–26 Feb 2007). Thirteen marked birds, visible from the road, were checked each day until a carcass was removed by scavengers or the feather pile became indiscernible because it was matted and reduced by rains. We calculated the mean decomposition time (time until they would no longer be counted as present) of these 13 birds using Kaplan-Meier survival analysis (SPSS 2000) and used the upper bound of the 95% confidence interval of mean survival time to calculate a conservative estimate of carcass turnover time.

Third, an estimate of the total riparian areas used by pigeons for roosting at night and at a similar elevation to the Robertson Creek site examined in the first step was obtained using GIS layers in ArcGIS (ESRI 2007). All contiguous stream courses fitting our criteria within the larger study area, supported with observations of dead or dying pigeons in their vicinity, were identified and the area along them was buffered with a 56.4-m strip (based on the effective strip width from program DISTANCE®, as detailed below) to calculate area. We did not include the high, dry, south-facing streambeds of the watershed as these areas are dominated by relatively short shrubs, lack tall oak trees, and are rarely used by Band-tailed Pigeons. Informal telephone interviews with land managers of the nearby U.S. Forest Service and private lands confirmed the presence of many dead and dying Band-tailed Pigeons within the study area.

We conservatively estimated the period during which mortality occurred to be 60 days (15 Jan to 15 Mar). The total number of Band-tailed Pigeons carcasses occurring during this time period within the study area was estimated using the formula below.

$$\text{Total pigeon carcasses} = D \cdot RA \cdot (1/MST) \cdot P,$$

where D = the density of pigeons (carcasses/ha) in the Robertson Creek census transect, RA = the total estimated riparian area within the study area, 1/MST is the turnover rate of dead carcasses (the inverse of the upper bound of the 95% confidence interval of mean survival time [MST]), and P = the length of the period during which pigeon mortality was significant.

The California Animal Health and Food Safety Laboratory System (CAHFS) and R. W. Gerhold, Wildlife Disease Section, University of Georgia, Athens, Georgia, evaluated the dead pigeons; the latter used an Inpouch TriTrichomonas Test pouch kit (Cover et al. 1994). Samples were collected at several times during the study and pigeons consistently showed diagnostic symptoms of infection by *T. gallinae* (caseous, obstructive lesions within the upper areas of the digestive tract; Cole 1999). Freshly dead pigeon carcasses (25) were collected, frozen, and deposited in the Museum of Vertebrate Zoology, University of California, Berkeley.

RESULTS

All Band-tailed Pigeons found dead or dying had clinical signs of trichomoniasis including low body weight, listlessness, caseous or cheesy, yellowish lesions in the mouth, throat, and around the beak, and tendency to fall over when forced to move (Stabler and Braun 1975, 1979; Cover et al. 1994). Laboratory test results were positive for *Trichomonas gallinae* and negative for West Nile virus (R. W. Gerhold and K. D. Hanni, pers. comm.).

We counted 373 dead pigeons over the 2.5-km transect surveyed along Robertson Creek on 7 February 2007. Based on the GPS coordinates of the birds, DISTANCE® calculated an effective (one-half) strip width of 28.2 m (μ in Buckland et al. 1993). We therefore used 56.4 m as the ArcGIS buffer function to calculate the area of the survey transect along the winding riparian corridor, producing an estimated density of dead birds of 26.45 birds/ha. We estimated 271.3 ha of comparable riparian habitat within the larger 52.7-km^2 study area. Assuming densities of dead birds comparable to that found on the transect conducted at Hastings, this yields a total of 7,177 pigeon carcasses detectable at any one point in time along the riparian corridors of the study area.

We observed relatively high densities of feral pigs (*Sus scrofa*), coyotes (*Canis latrans*), and raptors including Barn Owls (*Tyto alba*), Red-tailed Hawks (*Buteo jamaicensis*), and Cooper's Hawks (*Accipter cooperii*) in the census transect. Unsurprisingly, this resulted in relatively rapid estimated carcass turnover times. The mean time to carcass decomposition was 2.8 days with a 95% confidence interval of 2–10

days based on Kaplan-Meier survival analysis of 13 marked carcasses checked over an 18-day period in February 2007.

We assume the death rate was constant over the peak of the mortality event. The number of dead individuals was conservatively estimated to have turned over at least six times yielding a total estimate of 43,059 dead pigeons within the total study area during the 2-month period of peak mortality.

DISCUSSION

Mortality attributable to *T. gallinae* during winter 2006–2007 was high relative to other major causes of mortality of Band-tailed Pigeons. The estimated numbers of this species harvested over their entire range in the United States for 1999, 2000, 2004, and 2005 averaged 20,550 per year (USDI 2006a, b). Epizootic trichomoniasis in Band-tailed Pigeons has been reported previously (Cole 1999) with the largest prior estimate of mortality being 16,000 pigeons. A series of reports of trichomoniasis in Band-tailed Pigeons from northern California (USGS 1995, 2004, 2006) estimated 2,000, 2,000, and 300 deaths, respectively.

Our survival analysis assumes that mortality was constant over the period considered. It is possible, however, that we missed the period of peak mortality, as we did not immediately recognize the severity and extent of the die-off, and were spurred to conduct quantitative sampling some time after peak mortality may have occurred.

It is also likely the mortality extended much farther than we were able to confirm. U.S. Forest Service employees were not available to conduct searches for pigeons along the riparian areas in the nearby Ventana Wilderness, a large (~3,500 km^2) mostly inaccessible area that is similar to the habitat at Hastings Reservation. Mortality may also have extended well into the upper Carmel and Arroyo Seco watersheds of the Ventana Wilderness where large flocks of Band-tailed Pigeons are common in winter (Roberson and Tenny 2002). Thus, the total number of birds affected by the event within Monterey County may have been several times our estimate of ~43,000 birds.

The mortality event reported here is far in excess of what has been previously observed and is far more significant than hunting mortality over the species' North American range. Despite the die-off, flocks of pigeons remained common through late March within the study area.

ACKNOWLEDGMENTS

We thank B. J. Piculell and R. D. Drobek for assistance with surveying and R. W. Gerhold for confirming trichomoniasis. Testing was arranged by J. D. Cann (California Department of Fish and Game) and K. D. Hanni (Monterey County Health Department). ELW was supported by NSF grant IOB-0516851 to WDK.

LITERATURE CITED

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London, United Kingdom.

Cole, R. A. 1999. Trichomoniasis. Pages 201–206 *in* Field manual of wildlife diseases: general field procedures and diseases of birds (M. Friend and J. C. Franson, Editors). USDI, Geological Survey-BRD, Washington, D.C., USA.

Cover, A. J., W. M. Harmon, and M. W. Thomas. 1994. A new method for the diagnosis of *Trichomonas gallinae* infection by culture. Journal of Wildlife Diseases 30:457–459.

Davis, J., W. D. Koenig, and P. L. Williams. 1980. Birds of Hastings Reservation, Monterey County, California. Western Birds 11:113–128.

ESRI, Inc. 2007. ArcGIS. Version 9.2.2. Earth Systems Research Institute, Inc., Redlands, California, USA.

Keppie, D. M. and C. E. Braun. 2000. Band-tailed Pigeon (*Columba fasciata*). The birds of North America. Number 530.

Roberson, D. and C. Tenny. 2002. Monterey Birds. Second Edition. Monterey Peninsula Audubon Society, Monterey, California, USA.

SPSS Institute, Inc. 2000. SPSS for Windows. Version 10.0. SPSS Institute, Inc., Chicago, Illinois, USA.

Stabler, R. M. and C. E. Braun. 1975. Effect of virulent *Trichomonas gallinae* on the Band-tailed Pigeon. Journal of Wildlife Diseases 11:482–483.

Stabler, R. M. and C. E. Braun. 1979. Effects of a California derived strain of *Trichomonas gallinae* on Colorado USA Band-tailed Pigeons. California Fish and Game 65:56–58.

Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, J. R. B. Bishop, and T. A. Marques. 2006. DISTANCE 5.0. Release 2.0. University of St. Andrews, United Kingdom. http://www.ruwpa.st-and.ac.uk/distance (accessed 15 June 2007).

U.S. Department of the Interior (USDI). 2006a. Mi-

gratory bird hunting activity and harvest during the 1999 and 2000 hunting seasons—Final Report. USDI, Fish and Wildlife Service, Washington, D.C., USA.

U.S. DEPARTMENT OF THE INTERIOR (USDI). 2006b. Migratory bird hunting activity and harvest during the 2004 and 2005 hunting seasons: preliminary estimates. USDI, Washington, D.C., USA.

U.S. GEOLOGICAL SURVEY (USGS). 1995. Quarterly Wildlife Mortality Report April 1995 to June 1995. USGS, National Wildlife Health Center, Madison, Wisconsin, USA.

U.S. GEOLOGICAL SURVEY (USGS). 2004. Quarterly Wildlife Mortality Report April 2004 to June 2004. USGS, National Wildlife Health Center, Madison, Wisconsin, USA.

U.S. GEOLOGICAL SURVEY (USGS). 2006. Quarterly Wildlife Mortality Report April 2006 to June 2006. USGS, National Wildlife Health Center, Madison, Wisconsin, USA.

The Wilson Journal of Ornithology 120(3):606–610, 2008

Winter Ecology of Yellow Rails Based on South Carolina Specimens

William Post[1]

ABSTRACT.—Arthur T. Wayne collected 58 Yellow Rails (*Coturnicops noveboracensis*) during seven winters between 1903 and 1918 at one locality on the Atlantic coast in Charleston County, South Carolina. The collection represents the largest known series of Yellow Rails from a single wintering site and provides information about the winter ecology of this species. There was no evidence that Yellow Rail numbers varied between winters. The sex ratio was significantly biased toward females suggesting the occurrence of differential wintering. Yellow Rails were collected mainly in wet (freshwater) fields with short dense grass, the same features of Yellow Rail habitats in coastal Texas. Yellow Rails were consistently located in the same habitats as LeConte's Sparrow (*Ammodramus leconteii*). Two other grassland species, Henslow's Sparrows (*A. henslowii*) and Sedge Wrens (*Cistothorus palustris*), had habitat occupancy patterns significantly different from that of Yellow Rails. *Received 6 June 2007. Accepted 21 November 2007.*

The Yellow Rail (*Coturnicops noveboracensis*) has been studied in breeding areas (Peabody 1922, Terrill 1943, Stalheim 1974, Anderson 1977, Bookhout and Stenzel 1987, Gibbs et al. 1991, Robert and Laporte 1999, Popper and Stern 2000, Robert et al. 2000) and in captivity (Stalheim 1975). Historically, migratory populations of the Yellow Rail occupied a discontinuous breeding range from the Northwestern Territories to New Brunswick, Canada, south to the latitudes of Connecticut and Oregon, USA (Bookhout 1995), and wintered primarily on the coastal plain from North Carolina to Texas. Most information about the species in winter is from studies conducted on the Gulf coast of Texas (Grace et al. 2005), and little is known about Yellow Rails overwintering on the Atlantic coast. A series of 58 specimens collected at one locality in South Carolina between 1903 and 1918 provides information about patterns of occurrence, habitat use, and sex ratios in winter. The objective of this paper is to compare these data with that available from other areas of its wintering range.

METHODS

This paper is based on the field work of Arthur T. Wayne who, in 1903–1913, collected 56 Yellow Rails in Charleston County, South Carolina. I examined 36 of the skins and confirmed the information on their labels accurately reflected entries in his specimen ledgers, which are archived at the Charleston Museum. Additional data were contained in Wayne's correspondence and published papers. These sources provided the gender, collection date, and collection location of each specimen. The skins are not accompanied by habitat information, but Wayne recorded the name of the field where each bird was collected, and his letters and articles contained descriptions of the fields. I assume that each of Wayne's collecting trips involved about the same amount of time. He usually worked at one location each day and took 3–4 speci-

[1] Charleston Museum, 360 Meeting Street, Charleston, SC 29403, USA; e-mail: grackler@aol.com

mens. The primary or secondary sex ratios of Yellow Rail are unknown. The species is believed to be monogamous (Bookhout 1995) and I assume the sex ratio is approximately equal at the end of the breeding season

RESULTS

Wayne first discovered Yellow Rails wintering in South Carolina on 4 February 1898, when he obtained a cat (*Felis catus*)-captured bird, too mangled to preserve (Wayne 1910). The next Yellow Rail that Wayne encountered, also captured by a cat (19 Dec 1903), was a male (Wayne 1905; specimen #ATW 4529; Museum of Comparative Zoology #309649). Wayne then began searching appropriate habitats using hunting dogs (pointers) and from 1903 to 1913, collected 56 more Yellow Rails, all within 10 km of his house at Porcher's Bluff, Mt. Pleasant, Charleston County, South Carolina (32° 51′ 22″ N, 79° 46′ 49″ W).

Wayne collected and reported the gender of 56 Yellow Rails during seven winters in 1903–1913 (Table 1). Of these, 77% were females, representing a significant departure from a balanced sex ratio ($\chi^2 = 8.5$, df = 1, $P < 0.005$). His peak period was winter 1909–1910, when he collected 35 Yellow Rails, 83% of which were females, also representative of an unbalanced winter sex ratio ($\chi^2 = 8.5$, df = 1, $P < 0.005$). Sex ratios are based on birds that were removed from the same population. Forty-one of the 50 trips that Wayne made in 1909–1910 were to one field. Too few birds were collected in other years to examine the significance of any departure from a 1:1 ratio (Table 1). Wayne noted that four females he collected from 11 November to 10 December were molting.

The notes and papers of Wayne provide an idea of the habitats used by Yellow Rails. A main collecting site was "a low wet place of open land with a dense growth of short dead grass" (Wayne 1905:396–397). Wayne collected three other species in the same habitats as the rails: LeConte's Sparrows (*Ammodramus leconteii*), Sedge Wrens (*Cistothorus platensis*), and Henslow's Sparrows (*A. henslowii*).

Based on Wayne's notes, most Yellow Rails (32/41; 78%) occurred in the wettest of three sites (Table 2), as did LeConte's Sparrows (35/44; 80%). Henslow's Sparrows were collected most often in the driest of the fields (12/17;

TABLE 1. Occurrence of Yellow Rails and other grassland species in winter during 1903–1913 at Mt. Pleasant, South Carolina. Data represent only winters in which Yellow Rails were collected.

Winter	Period	Trips	Sites sampled	Yellow Rail			LeConte's Sparrow	Henslow's Sparrow	Sedge Wren
				Male	Female	Total			
1903–1904	19 Dec–27 Feb	7	3	4	4	8 (1.14)[a]	2 (0.29)	0	0
1904–1905	19 Nov–11 Feb	6	3	0	1	1 (0.17)	4 (0.67)	4 (0.67)	0
1906–1907	14 Nov–12 Jan	4	1	0	2	2 (0.50)	1 (0.25)	2 (0.50)	0
1907–1908	28 Nov–5 Feb	8	1	1	4	5 (0.63)	3 (0.38)	4 (0.50)	0
1909–1910	10 Nov–21 Mar	50	4	6	29[b]	35 (0.70)	38 (0.76)	1 (0.02)	15 (0.30)
1910–1911	30 Nov–6 Dec	14	4	2	2	4 (0.29)	1 (0.07)	2 (0.14)	10 (0.71)
1912–1913	19 Nov–18 Jan	15	3	0	1	1 (0.07)	9 (0.60)	0	8 (0.53)
All winters[c]		104	12	13	43[d]	56 (0.54)	92 (0.88)	13 (0.13)	33 (0.32)

[a] Number of birds/trip.
[b] Significantly more females than males were collected ($X^2 = 8.7$, df = 1, $P < 0.005$).
[c] Number of different sites over total period.
[d] Significantly more females than males were collected ($X^2 = 8.5$, df = 1, $P < 0.005$).

TABLE 2. Habitats used by wintering Yellow Rails and other species at Mt. Pleasant, South Carolina.

Species	Porcher's Rough Ground[a] 1909–1913 (57)[d]	Porcher's Myrtle Pasture[b] 1906–1918 (36)	Cat island[c] 1903–1911 (27)
Yellow Rail	32	2	7
LeConte's Sparrow	35	5	4
Henslow's Sparrrow	5	0	12
Sedge Wren	10	34	4

[a] Wet: two-layered vegetation (a dense layer of short graminoids and forbs interspersed with broom sedge).
[b] Moist to wet: three-layered vegetation (short grasses and sedges, broom sedge and wax myrtle).
[c] Moist to dry: primarily one-layered (short grasses and sedges and scattered clumps of broom sedge).
[d] Number of trips.

71%), where few Yellow Rails were collected (7/41; 17%). Most Sedge Wrens (34/48; 71%) were collected in sites with a mid-range of moisture, and with greater cover of shrubs. Only 5% (2/41) of the Yellow Rails occurred in habitat with shrubs. LeConte's Sparrows were collected on the same days at the same sites in each of the seven winters in which Yellow Rails occurred. Rails co-occurred with Henslow's Sparrows and Sedge Wrens in four and three winters, respectively. The habitat use pattern of Yellow Rails and LeConte's Sparrows did not differ from that expected under a null hypothesis ($G = 11.8$, df = 6, $P > 0.05$). However, I reject the null hypothesis that Yellow Rails had the same pattern of habitat use as Henslow's Sparrows ($G = 20.8$, df = 6, $P < 0.001$) and Sedge Wrens ($G = 13.0$, df = 6, $P < 0.05$).

DISCUSSION

Loomis (1891) collected four Yellow Rails (1 male, 1 female, 2 unknown gender) in 1887 in the Piedmont of South Carolina (Chester County), but Wayne (1905) did not find the species on the coast until 1898. Wayne collected Yellow Rails in seven winters over 11 years (1903–1913). Two apparent peaks occurred: one in winter 1909–1910 (35 Yellow Rails), and another in 1903–1904 (7). There were few differences between years when considering numbers of rails collected per trip (Table 1). For example, in winter 1909–1910, when Wayne collected 35 rails in 50 trips, the success rate (0.70 rails/trip) was not much greater than that obtained during 1907–1908, when only five Yellow Rails were collected in eight trips (0.63/trip; Table 1). Besides unequal effort between years, Wayne concentrated his work in fields where he frequently encountered Yellow Rails, curtailing visits to other sites. For example, in 1909–1910, 41 of 50 trips were to one field (Porcher's Rough Ground). Unequal effort between years and localities is also a source of bias when considering annual variation in LeConte's Sparrow populations. McNair and Post (2000) hypothesized that numbers of the latter species varied significantly between years, and they considered winters such as 1909–1910, when Wayne collected 38 LeConte's Sparrows, to be "incursion" years. Wayne's sampling was not random. If he obtained an unusual specimen, he intensified his search effort at the collection site. As in the case of Yellow Rails, when numbers collected are considered with effort, there was little difference between years. Wayne obtained four LeConte's Sparrows in winter 1904–1905 (0.67/trip), almost the same rate as in 1909–1910 when he collected 35 (0.70/trip; Table 1). Annual variation in the numbers of Yellow Rails and LeConte's Sparrows can be most parsimoniously explained by uneven collecting effort between years and among collection sites.

Few workers on the Atlantic coast have mentioned the habitats in which they found wintering Yellow Rails, but the sites for which descriptions are available appear to be similar to fields visited by Wayne. For example, the Beaufort-Morehead (North Carolina) airport, where ≥28 Yellow Rails were counted in 1 day during a controlled burn (Chapman 1969), was covered primarily by shorter vegetation such as panicgrass (*Panicum* spp.), interspersed with clumps of broom sedge (*Andropogon* spp.). Anderson (1977) suggested that Yellow Rails prefer drier portions of *Spartina* marshes (salinity not indicated) in winter. Wayne encountered Yellow Rails only in freshwater or low salinity sites, although he made numerous trips to salt marshes, as dem-

onstrated by the 381 Seaside Sparrows (*Ammodramus maritimus*) he collected.

Yellow Rails and LeConte's Sparrows consistently occurred in the same habitats, old-fields dominated by short vegetation such as panicgrass and by rushes (*Juncus* spp.). These fields appeared to have a secondary vegetative layer composed of broom sedge, which probably was more frequent at higher elevations. Some sites also had a third layer, composed of shrubs such as wax myrtle (*Myrica cerifera*) and groundsel (*Baccharis halimifolia*). Landowners periodically cattle-grazed and burned the fields, and Wayne's notes imply that shrubs were low and scattered. Yellow Rails and LeConte's Sparrows both occurred most often in wetter, more open fields (Table 2). Henslow's Sparrows and Sedge Wrens were most common in drier sites. Sedge Wrens were frequently collected in fields that had shrubs, but few Yellow Rails or *Ammodramus* sparrows were collected there (Table 2). Based on Wayne's studies, the winter habitats of Yellow Rails in South Carolina correspond to those in coastal Texas, where the most constant features of all Yellow Rail locations are dense vegetative cover and low plant height (Grace et al. 2005).

Wayne collected a significantly larger number of female than male Yellow Rails, a disparity which suggests that males and females overwinter at different latitudes or use different habitats. Disproportionate numbers of females of another rallid, the American Coot (*Fulica americana*), have been found wintering farther south than males (Eddleman 1983, Brisbin and Mowbray 2002). Wayne's work demonstrates sexual segregation in one region and in different habitats. Limited data suggest sex ratios favor male Yellow Rails in areas north of South Carolina. In a series of 17 winter specimens collected north of Chesapeake Bay (39° 32′ 55″ N), the sex ratio was 9 males:2 females; the comparable ratio for birds collected south of Chesapeake Bay (excluding South Carolina) was 3 males:3 females. These data are too few to examine statistically, but they suggest that in comparison to sex ratios found by Wayne, male Yellow Rails do not migrate as far south as females. If differential wintering is widespread, it could have implications for management practices. Female-biased dispersal may lead to male-biased sex ratios in breeding areas, increasing vulnerability to extinction of small or isolated populations, or populations at the periphery of a species' range (Dale 2001). This suggests that one objective of future research might be to examine how Yellow Rail sex ratios are affected by prescribed fires and grazing in different overwintering areas (Mizell 1998, Grace et al. 2005, Baldwin et al. 2007).

ACKNOWLEDGMENTS

The following museums provided access to their collections: American Museum of Natural History, British Museum, Charleston Museum, Field Museum, Museum of Comparative Zoology (Harvard), Philadelphia Academy of Science, and Smithsonian Institution. The American Museum of Natural History and Museum of Comparative Zoology kindly provided copies of Wayne's letters. This paper benefited from discussions with D. B. McNair. D. R. C. Prescott and an anonymous reviewer provided useful comments enabling me to improve the manuscript.

LITERATURE CITED

Anderson, J. M. 1977. Yellow Rail (*Coturnicops noveboracensis*). Pages 66–70 *in* Management of migratory shore and upland game birds in North America (G. C. Sanderson, Editor). International Association of Fish and Wildlife Agencies, Washington, D.C., USA.

Baldwin, H. Q., J. B. Grace, W. C. Barrow Jr., and F. C. Rowher. 2007. Habitat relationships of birds overwintering in a managed coastal prairie. Wilson Journal of Ornithology 119:189–197.

Bookhout, T. A. 1995. Yellow Rail (*Coturnicops noveboracensis*). The birds of North America. Number 139.

Bookhout, T. A. and J. R. Stenzel. 1987. Habitat and movements of breeding Yellow Rails. Wilson Bulletin 99:441–447.

Brisbin Jr., I. L. and T. B. Mowbray. 2002. American Coot (*Fulica americana*). The birds of North America. Number 697.

Chapman, F. L. 1969. Yellow Rails at Beaufort, N.C. Chat 33:103.

Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos 92: 344–356.

Eddleman, W. R. 1983. A study of migratory American Coots, *Fulica americana*. Dissertation. Oklahoma State University, Stillwater, USA.

Gibbs, J. P., W. G. Shriver, and S. M. Melvin. 1991. Spring and summer records of the Yellow Rail in Maine. Journal of Field Ornithology 62:509–516.

Grace, J. B., L. K. Allain, H. Q. Baldwin, A. G. Billock, W. R. Eddleman, A. M. Given, C. W. Jeske, and R. M. Moss. 2005. Effects of prescribed fire in the coastal prairies of Texas. USDI, Geological Sur-

vey and Fish and Wildlife Service, Region 2. Open-File Report 2005-1287. htpp://www.nwrc.usgs.gov/facshts/2005-1287-fire-in-coastal-texas-report.pdf.

Loomis, L. M. 1891. A further review of the avian fauna of Chester County, South Carolina. Auk 8: 49–59,167–173.

McNair, D. B. and W. Post. 2000. Historical winter status of three upland *Ammodramus* sparrows in South Carolina. Studies in Avian Biology 21:32–38.

Mizell, K. L. 1998. Effects of fire and grazing on Yellow Rail habitat in a Texas coastal marsh. Dissertation. Texas A&M University, College Station, USA.

Peabody, P. B. 1922. Haunts and breeding habits of the Yellow Rail *Coturnicops noveboracensis*. Journal of the Museum of Comparative Oology 2: 33–44.

Popper, K. J. and M. A. Stern. 2000. Nesting ecology of Yellow Rails in southcentral Oregon. Journal of Field Ornithology 71:460–466.

Robert, M. and P. Laporte. 1999. Numbers and movements of Yellow Rails along the St. Lawrence River. Condor 101:667–671.

Robert, M., P. Laporte, and R. Benoit. 2000. Summer habitat of Yellow Rails, *Coturnicops noveboracensis*, along the St. Lawrence River, Quebec. Canadian Field-Naturalist 114:628–635.

Stalheim, P. S. 1974. Behavior and ecology of the Yellow Rail (*Coturnicops noveboracensis*). Thesis. University of Minnesota, Minneapolis, USA.

Stalheim, P. S. 1975. Breeding and behavior of captive Yellow Rails. Aviculture Magazine 81:133–141.

Terrill, L. M. 1943. Nesting habits of the Yellow Rail in Gaspe County, Quebec. Auk 60:171–180.

Wayne, A. T. 1905. Notes on certain birds taken or seen near Charleston, South Carolina. Auk 22: 395–400.

Wayne, A. T. 1910. Birds of South Carolina. Contributions from the Charleston Museum I. Daggett Printing Company, Charleston, South Carolina, USA.

The Wilson Journal of Ornithology 120(3):610–613, 2008

Nest Raising by Red-crowned Cranes in Response to Human-mediated Flooding at Zhalong Nature Reserve, China

Qiang Wang[1,2,3] and Feng Li[3,4]

ABSTRACT.—Water was released from a reservoir in May 2005 to restore the wetland of international importance at Zhalong, China. As a result, the water level on the floodplain rose rapidly. A pair of Red-crowned Cranes (*Grus japonensis*) was observed raising their nest to avoid submersion and loss of eggs. The nest and two eggs were tended by both adults, but the eggs did not hatch. Hatching failure may have resulted from low egg temperatures due to addition of wet and new nesting materials, and reduction of incubation time during the flooding event. Reservoir discharge should avoid the breeding period of waterbirds and discharge rates should be reduced. *Received 29 May 2007. Accepted 14 November 2007.*

Water level is an important factor affecting habitat selection by waterfowl (Kingsford and Johnson 1998, Timoney 1999, Adamo et al. 2004, Bradter et al. 2005), and can have both positive and negative effects on breeding and survival of waterbirds (Poiani 2006). Floods can increase food resources for some waterbirds and subsequently increase their chances of successful breeding (Nielsen and Gates 2007). However, floods can also lead to nesting failure (Borad et al. 2002, Mukherjee et al. 2002, Sanders and Maloney 2002, Gilbert and Servello 2005).

The Red-crowned Crane (*Grus japonensis*) is classified as a globally endangered species with a total population of ~2,000 birds (Meine and Archibald 1996). There is little information regarding the impact of floods on breeding success of this species but, floods were a major cause for breeding failure of the Indian Sarus Crane (*Grus antigone antigone*) with 12.2% of egg losses attributed to high water (Borad et al. 2002). Mukherjee et al. (2002) reported that a pair of Indian Sarus Cranes attempted to raise the nest platform by adding nest materials in response to flooding. This nest eventually became submerged and the eggs were lost.

Red-crowned Cranes nest within Zhalong

[1] Northeast Institute of Geography and Agricultural Ecology, CAS, Changchun, 130012, China.

[2] Graduate School, CAS, Beijing, 1300039, China.

[3] Department of Zoology, Northeast Forestry University, Harbin, 150040, China.

[4] Corresponding author; e-mail: lifeng_1956@126.com

FIG. 1. Red-crowned Crane nest before flooding, Zhalong Nature Reserve, China.

FIG. 2. Red-crowned Crane nest during flooding, Zhalong Nature Reserve, China.

Nature Reserve in China, a Ramsar wetland area of international importance. Increased demand for irrigation water for agriculture upriver from Zhalong Nature Reserves can lead to lack of water in the wetland, endangering local waterbirds (Lemly et al. 2000). The local government in 2005 decided to discharge water from a reservoir to recharge the wetland prior to the main period of irrigation. There is little recorded information regarding the impact of flooding on nesting behavior of Red-crowned Cranes. The objective of this paper is to report on observations of a pair of cranes raising their nest when flooding occurred.

OBSERVATIONS

We observed a pair of Red-crowned Cranes raising their nest as flood waters approached in the core zone of Zhalong Nature Reserve (123° 47′–124° 37′ E, 46° 52′–47° 32′ N) in western Heilongjiang Province of northeastern China in May 2005. We discovered and measured the nest on 9 May 2005 when the nest height was 23 cm with an inner diameter of 46 cm and an outer diameter of 130 cm; there were 2 eggs (Fig. 1). The nest was in a reed (*Phragmites australis*) floodplain marsh; the marsh vegetation consisted of reed, cattail (*Typha angustifolia*), and common bulrush (*Scirpus planiculmis*). The vegetation in the vicinity had been harvested the previous winter, leaving only stubble ~20 cm high (Fig. 1). The nest was built of dry, long reed stems on stubble in 15 cm of water. There was a shallow water pond 6 m northwest of the nest; the water depth in the pond was ~35 cm and its surface area was ~12 m^2. The nest was ~80 m from a river, where fishermen in row boats frequently passed.

The water level at the nest site increased rapidly beginning on 10 May as water from an up stream reservoir was released. We observed the Red-crowned Crane pair from an elevated location 1.2 km from the nest using a monocular telescope. The cranes continuously submerged their heads to collect below water material, flicking the material to eliminate water and mud before using it to raise the nest. We revisited the site at 1630 hrs and measured the raised nest; the nest height was 62 cm with an inner diameter of 41 cm and an outer diameter of 66 cm. The water depth adjacent to the nest was ~56 cm. We moved some dry reeds to the nest site, before resuming observation on 11 May. The pair continued to add material to the nest. We approached the nest at 0740 hrs and found the cranes had not used the dry, long reeds which we had placed there earlier. The new nest materials were primarily wet cattail stubble (with attached roots), and short stems of reed and common bulrush. We again measured the nest; the nest height had increased to 71 cm with an inner diameter of 44 cm and an outer diameter of 79 cm (Fig. 2). The water depth next to the nest was ~63 cm, and the inner and outer diameters were larger than when measured on 10 May (Fig. 3). We checked the nest on 22 May, 8 June, and 15 June, but the two eggs did not hatch. Eight- to 10-day-old dead embryos were found in the eggs on 15 June.

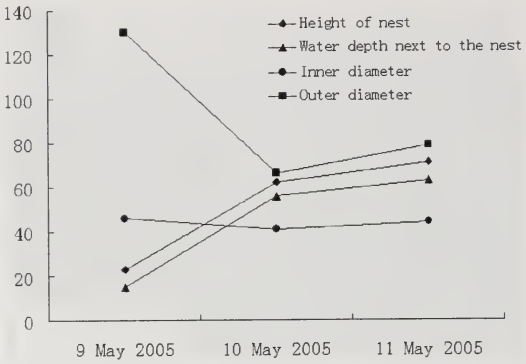


FIG. 3. Nest measurements (cm) by date, Zhalong Nature Reserve, China.

DISCUSSION

The average air temperature in Zhalong Nature Reserve was 14.4° C and average water temperature was 11.6° C in May from 1981 to 1990 (Wu 1999). We hypothesize that internal egg temperatures were too low, especially at night, as a result of the added wet nest materials, and that incubation time was shortened during flooding, resulting in embryo death. Selection of nesting materials changed during the flooding. Red-crowned Cranes typically choose dry, long reed stems to build their nests (Wu 1999). We do not know why this pair of Red-crowned Cranes chose wet vegetation growing next to the nest instead of dry vegetation placed there by humans. It is possible that water levels could have affected the birds' choice of nesting materials as reported by Kuyt (1995) for Whooping Cranes (*Grus americana*).

Nesting failure by the pair of Red-crowned Cranes observed following human-mediated flooding suggests better water management practices are needed at Zhalong Nature Reserve. Discharging large amounts of water at a high rate during incubation or when chicks are small can drastically affect hatching success and chick survival. Releasing excess water in spring prior to egg-laying allows Red-crowned Cranes and other birds time to adjust to higher water levels, and should still provide protection from predators (Picman 1988, Picman et al. 1993). Similar results would likely also occur if water was released at a slower rate. However the amount of water needed for agriculture is large in spring. Rainfall is plentiful in Zhalong Nature Reserve in autumn (Wu 1999) and there is little need for water for agriculture. Releasing water following the nesting season when chicks are larger is likely to reduce negative impacts, and mitigate the conflict for water between wetland restoration and agriculture. The objective of the water release was to re-flood the wetland following use for agriculture. However, the needs of waterbirds and other wildlife using the wetland should be considered regarding the amount and speed of water discharge.

ACKNOWLEDGMENTS

Our research was supported by National Natural Science Foundation of China (Warrant No. 30370221) and the International Crane Foundation. We thank F. S. Li for helpful comments. We also thank Y. M. Zhang, Y. J. Cai, J. G. Fu, and Y. B. Ba for help in the investigation. We are grateful to Zhalong National Nature Reserve for permission and access to conduct this study. M. A. Hayes and C. D. Littlefield provided helpful comments which improved the clarity of the original manuscript.

LITERATURE CITED

Adamo, M. C., L. Puglisi, and N. E. Baldaccini. 2004. Factors affecting Bittern *Botaurus stellaris* distribution in a Mediterranean wetland. Bird Conservation International 14:153–164.

Borad, C. K., A. Mukherjee, S. B. Patel, and B. M. Parasharya. 2002. Breeding performance of Indian Sarus Crane *Grus antigone antigone* in the paddy crop agroecosystem. Biodiversity and Conservation 11:795–805.

Bradter, U., S. Gombobaatar, C. Uuganbayar, T. E. Grazia, and K. M. Exo. 2005. Reproductive performance and nest-site selection of White-naped Cranes *Grus vipio* in the Ulz River Valley, northeastern Mongolia. Bird Conservation International 15:313–326.

Gilbert, A. T. and F. Servello. 2005. Water level dynamics in wetlands and nesting success of Black Terns in Maine. Waterbirds 28:181–187.

Kingsford, R. T. and W. Johnson. 1998. Impact of water diversions on colonially-nesting waterbirds in the Macquarie marshes of arid Australia. Colonial Waterbirds 21:159–170.

Kuyt, E. 1995. The nest and eggs of the Whooping Crane, *Grus americana*. Canadian Field-Naturalist 109:1–5.

Lemly, A. D., R. T. Kingsford, and J. R. Thompson. 2000. Irrigated agriculture and wildlife conservation: conflict on a global scale. Environmental Management 25:485–512.

Meine, C. D. and G. W. Archibald. 1996. The cranes: status survey and conservation action plan. IUCN, Gland. Switzerland, and Cambridge, United Kingdom.

Mukherjee, A., C. K. Borad, and B. M. Parasharya. 2002. Breeding performance of the Indian Sarus Crane in the agricultural landscape of western India. Biological Conservation 105:263–269.

Nielsen, C. L. R. and R. J. Gates. 2007. Reduced nest predation of cavity-nesting Wood Ducks during flooding in a bottomland hardwood forest. Condor 109:210–215.

Picman, J. M. 1988. Experimental study of predation on eggs of ground-nesting birds: effects of water depth and distance from edge. Condor 90:124–131.

Picman, J. M., M. L. Milks, and M. Leptich. 1993. Patterns of predation on passerine nests in marshes: effects of water depth and distance from edge. Auk 110:89–94.

Poiani, A. 2006. Effects of floods on distribution and reproduction of aquatic birds. Advances in Ecological Research 39:63–83.

Sanders, M. D. and R. F. Maloney. 2002. Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. Biological Conservation 106:225–236.

Timoney, K. 1999. The habitat of nesting Whooping Cranes. Biological Conservation 89:189–197.

Wu, C. S. 1999. Study and management on resources in Zhalong National Nature Reserve. Northeast Forestry University Press, Harbin, China.

The Wilson Journal of Ornithology 120(3):613–617, 2008

White-winged Diuca Finch (*Diuca speculifera*) Nesting on Quelccaya Ice Cap, Perú

Douglas R. Hardy[1,3] and Spencer P. Hardy[2]

ABSTRACT.—We found evidence of birds nesting directly on glacier ice of the Quelccaya Ice Cap in the Cordillera Vilcanota, Perú at elevations up to 5,300 m. Observations during June and July over several years consisted of numerous nests not *in situ* having obviously fallen from the steep and dynamic, retreating glacier margin. A typical nest was a bulky structure of grass and twigs with a dry mass of 160 g. The inner cup was nicely formed and lined with fine grass, measuring 6–7 cm in diameter and 4–5 cm deep. Feathers and entire wings of White-winged Diuca Finch (*Diuca speculifera*) were observed in association with the nests; this was the passerine species most commonly seen in the area. The evidence indicates the glacier nests were built and used by White-winged Diuca Finch, probably during the Austral autumn when on-site automated measurements indicate the wet season ends and air temperatures have not yet decreased. This is the first well-documented case of high-elevation avian nesting on glacier ice. *Received 30 November 2006. Accepted 26 December 2007.*

Some birds are well adapted to environments which are seasonally dominated by snow or sea ice, but birds are not generally associated with glaciers. Only the Emperor Penguin (*Aptenodytes forsteri*) is known to routinely nest on ice, typically frozen sea-ice (i.e., fast-ice) but at times in association with ice shelves derived from glaciers (Kooyman 1993). Transient birds have been observed passing over mountain glaciers at high elevations outside the polar regions or discovered after succumbing to harsh environmental conditions (Krajick 2002; L. G. Thompson, pers. comm.). However, glacier surfaces are usually cold, actively changing through accumulation and ablation, and at times wet; conditions that are poorly suited for nesting and raising young birds.

The ornithological literature contains only one detailed account of nesting on a glacier. This was the unusual circumstance where glaciers advancing into Alaska's Prince William Sound overran a Black-legged Kittiwake (*Rissa tridactyla*) colony (Irons 1988). Previously-used nest sites were unavailable and 77 kittiwake nests were constructed on the glacier face. All of these nests failed due to ablation and/or meltwater runoff which either dislodged the nests or caused them to disintegrate (Irons 1988; D. B. Irons, pers. comm.).

The objective of this paper is to present evidence of nesting by White-winged Diuca Finch (*Diuca speculifera*) directly on glacier ice of the Quelccaya Ice Cap in Cuzco De-

[1] Climate System Research Center, Geosciences Department, University of Massachusetts, Amherst, MA 01003, USA.

[2] Marion W. Cross School, Norwich, VT 05055, USA.

[3] Corresponding author;
e-mail: dhardy@geo.umass.edu

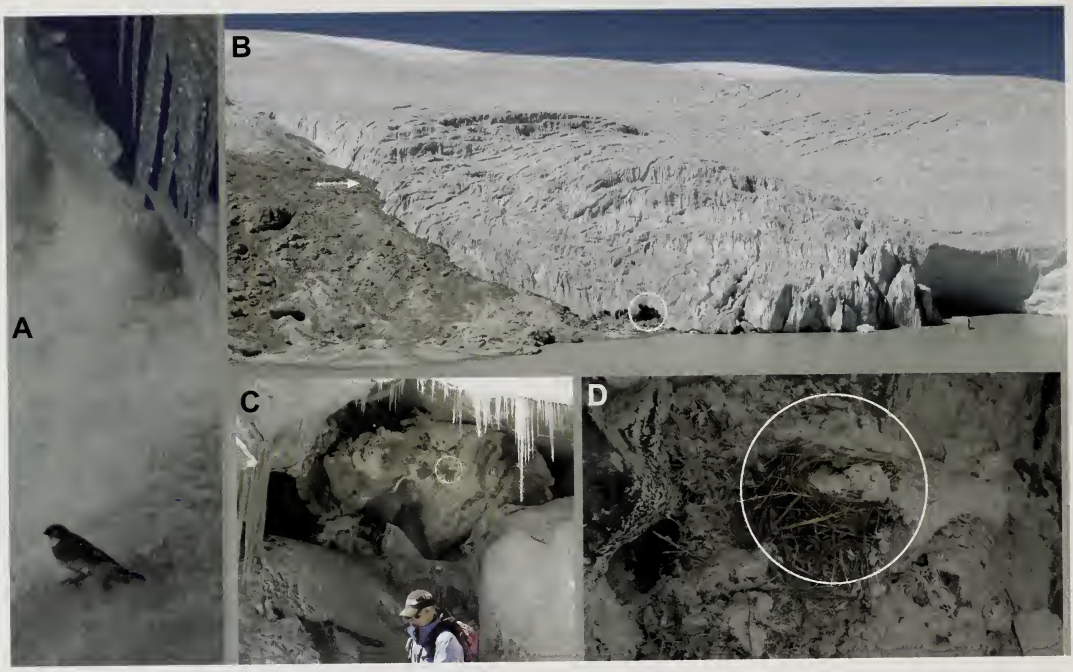


FIG. 1. (A) White-winged Diuca Finch on Quelccaya Ice Cap at ~5,200 m on 23 June 2007, (B) the same glacier in June 2005 with arrow indicating the approximate location of the first nest observation in 2005 and the nest described in text. Circled area of margin just above the proglacial lake is enlarged in (C) looking under the ice. The circle on (C) encloses a nest which is likely *in situ*, 3 m above rock surface with enlarged view in (D); note silt from meltwater runoff.

partment, Perú (14° S, 71° W). Observations were made over several years during the Austral winter (Jun–Jul) in the course of conducting glacier and climate research on the ice cap. This is the first well-documented case of high-elevation avian nesting on a glacier, corroborating a second-hand report of "ice cave" nesting by White-winged Diuca Finch (Johnson 1967).

OBSERVATIONS

During June 2005, while exploring the retreating Quelccaya Ice Cap margin, we came upon a nest which appeared to have fallen recently from the glacier (within weeks-months). Several other older nests were observed nearby including one in a cave under the ice margin (Fig. 1). More extensive nest searches were conducted in 2006 and 2007 along ~1,500 m of glacier margin, resulting in location of numerous nests. Most were along two sections with respective lengths of 350 and 530 m, elevation ranges of 50 and 100 m, and upper elevations of 5,200 and 5,300 m. Searches were restricted to this 1,500 m section; the extent to which this is representative of the Quelccaya Ice Cap is unknown. However, nesting on the ice cap has likely not been limited to the last 3 years as L. G. Thompson has occasionally observed nests over the past ~30 years (pers. comm.).

Nest remains were most often found on rocks at the base of near-vertical sections of ice margin. At least 14 nests were found in 2006 and at least 16 in 2007. These varied in apparent age from weeks (i.e., previous breeding season) to several years and the 2007 count almost certainly includes some found the previous year. Two of the freshest nests in 2006 were only 3 m apart.

Typically, sections of glacier margin with nest remains were nearly vertical, somewhat grooved or fluted, and ~5–10 m high. Overhanging icicles and steeply-sloping rock below the margin made access to some nest remains difficult, and nests still attached to the glacier could have been overlooked. One nest was found on the glacier 22 m from the mar-

FIG. 2. (A) Dislodged nest along Quelccaya Ice Cap margin found on 15 July 2006 in inverted position within 1 m of vertical ice wall at 5,190 m. The nest was not present the previous year (26 Jun 2005), although a different residual nest was found ~10 m distant. The dark bar on the field book cover is 1.25 × 9.5 cm. (B) Another dislodged nest in position found, 23 Jun 2007 at 5,230 m; note feathers and 13-cm pen for scale.

gin, below a steep, step-like section of ice (i.e., not *in situ*).

Some nests were entirely intact when found, while others were disintegrating or partially buried by sediment; however, almost all nests were not *in situ* (cf. Fig. 1D). Net retreat of the ice margin is roughly 1 m/year or more along this part of the Quelccaya Ice Cap and nests constructed on the steeply-sloping margin could only be observed *in situ* within a brief interval following construction (i.e., breeding season) prior to falling. Evidence for this interpretation is that several nests were found in inverted position and, in almost every case, a vertical trace of nest material was observed above the nest remains, frozen to the ice.

Remains of varying ages indicate multi-year occupation of favorable sites along the ice margin suggesting that reproductive efforts on the ice cap are successful. In addition, we observed fecal sacs in one of the fresh nests, presumably from nestlings just prior to fledging. No off-glacier nesting evidence was found despite searching areas adjacent to the glacier.

Several nests appeared entirely intact and the following is based upon one of the freshest-appearing nests observed in 2006. Nests were bulky structures of grass and twigs with a deep, well-made inner cup (Fig. 2). It appears that a rough platform is initially constructed (32 × 18 cm), which roughly tapers upward and becomes increasingly well-woven towards the top (13 cm outer diameter). Only this better-woven upper portion was found in some cases. The inner cup measured ~6.5 cm in diameter and was 4.6 cm deep. Overall dry mass of the nest (Fig. 2A) was 160 g. Nests consisted of woven grass (~80–90%), particularly the locally abundant *Calamagrostis chrysantha*. The inner cup was lined with finer grass and feathers were observed in or adjacent to some nest remains (Fig. 2B). Analysis by Carla Dove at the Smithsonian Institution revealed feathers of Rufous-bellied Seedsnipe (*Attagis gayi*), Andean Goose (*Chloephaga melanoptera*), and tail feathers of White-winged Diuca Finch. This diverse assemblage suggests that nests are lined with feathers recovered from the surrounding landscape. No evidence of camelid fleece was seen in any nest (cf. Johnson 1967).

DISCUSSION

Although indirect, all evidence indicates that Quelccaya glacier nests were built and used by White-winged Diuca Finch. Little information exists on nesting habits of this species from anywhere in the Andes although Johnson (1967: 368) reported that in the Parinacota area of

Chile, a White-winged Diuca Finch nest was found "on the ground beneath some loose stones on a hillside." In lieu of breeding-season observations of White-winged Diuca Finches at Quelccaya, our deduction is based upon their local presence, feathers, and the species known association with glaciers.

Small groups of White-winged Diuca Finches of unknown age class were frequently observed among rocky moraine surfaces and bogs in the area. This species is known to not typically retreat northward or to lower elevations during winter (Johnson 1967, 1972). On one occasion in June 2007, while we were investigating an apparent roosting site within a crack of the glacier, a flock of ~20 White-winged Diuca Finches began gathering late in the afternoon at the glacier margin, both on and off the glacier (Fig. 1). The birds acted disturbed by our presence in contrast to their behavior during diurnal feeding.

Several feathers observed in proximity to the nests were White-winged Diuca Finch wing or tail feathers. In addition, two nearly-entire wings (chord = 105 mm) of White-winged Diuca Finch were found on the ice at a 2007 nest site. No feathers were found from other passerine species (e.g., ground tyrants [*Muscisaxiola spp.*]) observed in close proximity to the glacier.

White-winged Diuca Finch is the only species to be repeatedly associated in the ornithological literature with Western Hemisphere glaciers. Niethammer (1953) observed an estimated 100 White-winged Diuca Finches gathering for the night inside a glacier crevasse at Chacaltaya (5,200 m) Bolivia in midsummer. He also collected one male specimen on 20 December in breeding condition with enlarged testes (6 × 4 mm vs. ~3 mm for another specimen collected in late August). A second association between White-winged Diuca Finch and glaciers was in the mid-1960s when P. R. Parker of the Chacaltaya Astrophysical Observatory found a nest "in an ice cave" at 5,300 m, leading Johnson (1967:368) to postulate the species "quite possibly nests at a higher altitude than any other passerine form." Subsequently, several sources mention that White-winged Diuca Finch has been recorded roosting in glacier fissures (Meyer de Schauensee 1970), glacier crevasses (Ridgely and Tudor 1989) or glacier cracks (Fjeldså and Krabbe 1990).

Relatively little is known about the timing of White-winged Diuca Finch nesting in Perú or elsewhere. Johnson (1967) suggested this species nested after the summer rains in the Parinacota region (Chile–Bolivia) where White-winged Diuca Finches were present all year. Immature White-winged Diuca Finches in Bolivia were noted by Fjeldså and Krabbe (1990) during July and August (La Paz), and August (Cochabamba). These findings are consistent with the Quelccaya situation, where climatic conditions present multiple difficulties for breeding birds, especially snow and low temperature (cf. Hendricks and Norment 1992, Martin and Wiebe 2004).

We began operating an automated weather station (AWS) in 2003 at the ice cap summit, ~3 km east of the nest sites and ~500 m higher in elevation. These data permit a close approximation of the climate in which nest building, incubation, and rearing of nestlings occurs on the glacier.

Pronounced seasonality of precipitation at Quelccaya typically features considerable and frequent snowfall from late September to early-mid April. During this wet season, 2 m or more of snow accumulates at the ice cap summit but, at the slightly lower elevation margin, ablation predominates; meltwater flows off during the day and freezes at night. Some precipitation at these nest sites (5,150–5,300 m) may be in the form of rain, as they are close to a rising atmospheric freezing level (Thompson et al. 1993, Bradley et al. 2006). This would impact the bird's exposure to moisture, thermal regulation, food availability, and other factors, and the viability of glacier nesting in the area.

Diurnal fluctuations in air temperature at Quelccaya are greater than the annual variation. By assuming a constant environmental lapse rate, summit AWS measurements can be adjusted to the elevation of nesting site, revealing average daily minima of −3.1° and −6.3° C during the wet and dry seasons, respectively. Thus, air temperature is low during the night throughout the year with extreme radiational cooling whenever cloud cover is low (especially in the dry season). Maxima for the same periods reach 2.9° and 0.9° C at the nesting sites.

Successful nesting in this dynamic environment and extreme climate requires not only

thermal and mechanical adaptations to the ice substrate, but also careful timing within the seasonal cycle of climate. The AWS data suggest that Quelccaya glacier nesting by White-winged Diuca Finch most likely occurs as the wet season concludes in April when nesting sites become exposed and drier, as the transient snow line elevation rises. Daily mean temperatures decrease after March as decreasing cloud cover results in colder nights, but the decrease in daily maximum is considerably more gradual until June (DRH, unpubl. data). Young finches had apparently fledged in each of the past 3 years by this date.

Note Added in Proof.—Quelccaya fieldwork during June 2008 provided additional observations. The first nests clearly *in situ* were observed on the glacier, in locations and orientation as hypothesized. One contained two abandoned eggs consistent in size and color for White-winged Diuca Finch (Johnson 1967). Also, a single off-glacier nest, similar to that described above, was found *in situ* under boulders ~500 m from the glacier. A late-afternoon gathering of 20–30 White-winged Diuca Finch was again observed, 30–60 min prior to sundown, at the same section of fractured glacier margin where this behavior was observed in 2007. Several roosts were located nearby, all entirely within (vs. beneath) the glacier. One expedition member observed and photographed White-winged Diuca Finch roosting at the site prior to sunrise (J. A. Castañeda Gil, pers. comm.). Supplemental material on glacier-nesting White-winged Diuca Finch at Quelccaya Ice Cap is available at http://www.geo.umass.edu/climate/quelccaya/diuca.html.

ACKNOWLEDGMENTS

This material is based upon work supported by the National Science Foundation and NOAA Office of Global Programs, Climate Change Data and Detection Program (Grant No. 0402557, awarded to DRH). The able field assistance of Mathias Vuille, Carsten Braun, and D. R. Dockstader, along with Mountain Guide Felix Vicencio and staff, is gratefully acknowledged. Initial discussion of these observations with Jon Fjeldså, Alvaro Jaramillo, and M. A. Plenge was helpful. Carla Dove at the Smithsonian Institution (Washington, D.C.) undertook feather identification in her laboratory and provided considerable enthusiasm. We also thank G. A. Clark, who encouraged preparation of the manuscript and provided insightful comments on an earlier draft. Two anonymous reviewers considerably improved the manuscript.

LITERATURE CITED

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. Science 312:1755–1756.

Fjeldså, J. and N. Krabbe. 1990. Birds of the High Andes. Zoological Museum, University of Copenhagen, and Apollo Books, Svendborg, Denmark.

Hendricks, P. and C. J. Norment. 1992. Effects of a severe snowstorm on subalpine and alpine populations of nesting American Pipits. Journal of Field Ornithology 63:331–338.

Irons, D. B. 1988. Black-legged Kittiwakes nest on advancing glacier. Wilson Bulletin 100:324–325.

Johnson, A. W. 1967. The birds of Chile and adjacent regions of Argentina, Bolivia and Perú. Volume 2. Platt Establecimientos Gráficos, Buenos Aires, Argentina.

Johnson, A. W. 1972. The birds of Chile and adjacent regions of Argentina, Bolivia and Perú, Supplement. Platt Establecimientos Gráficos, Buenos Aires, Argentina.

Kooyman, G. L. 1993. Breeding habitats of Emperor Penguins in the western Ross Sea. Antarctic Science 5:143–148.

Krajick, K. 2002. Melting glaciers release ancient relics. Science 296:454–456.

Martin, K. and K. L. Wiebe. 2004. Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. Integrative and Comparative Biology 44:177–185.

Meyer de Schauensee, R. 1970. A guide to the birds of South America. Academy of Natural Sciences of Philadelphia and Livingston Publishing Company, Wynnewood, Pennsylvania, USA.

Niethammer, G. 1953. Zur Vogelwelt Boliviens. Bonner Zoologische Beiträge 4:195–303.

Ridgely, R. S. and G. Tudor. 1989. The birds of South America. Volume 1. The oscine passerines. University of Texas Press, Austin, USA.

Thompson, L. G., E. Mosley-Thompson, M. Davis, P.-N. Lin, T. Yao, M. Dyurgerov, and J. Dai. 1993. "Recent warming": ice core evidence from tropical ice cores with emphasis on Central Asia. Global and Planetary Change 7:145–156.

The Wilson Journal of Ornithology 120(3):618–619, 2008

Nest Success and Nest Predation of the Endangered Rota White-eye (*Zosterops rotensis*)

Lainie Berry[1,3] and Estanislao Taisacan[2]

ABSTRACT.—The Rota White-eye (*Zosterops rotensis*) is an endangered species endemic to the island of Rota in western Micronesia. We monitored eight nests from 2003 to 2005, four of which produced at least one fledgling. Clutch size was two in each of five nests that were counted; the average number of fledglings from successful nests was 1.5 (n = 4). We filmed six nests and captured two nest predation events on video. A Mariana Crow (*Corvus kubaryi*), which is also an endangered species, was filmed taking nestlings from one white-eye nest. Another nest containing eggs was depredated by a rat (*Rattus* spp.); however, this may have occurred after the nest was abandoned due to the presence of the camera. *Received 24 September 2007. Accepted 16 January 2008.*

The Rota White-eye (*Zosterops rotensis*) is endemic to the island of Rota, Northern Mariana Islands, in western Micronesia (14° 09′ N, 145° 12′ E) and is listed as federally endangered (USDI 2004). The population is currently limited to ~250 ha of mature limestone forest above 150 m elevation (Fancy and Snetsinger 2001). Island-wide surveys yielded a population estimate of ~10,000 white-eyes in 1982 (Engbring et al. 1986); surveys in 1996–1999 indicate the population has since decreased to ~1,000 individuals (Amidon 2000, Fancy and Snetsinger 2001). Predation by the introduced Black Drongo (*Dicrurus macrocerus*) or rats (*Rattus* spp.) is a possible cause of the decline of the Rota White-eye (Craig and Taisacan 1994, Fancy and Snetsinger 2001). Direct evidence on causes of the decline is lacking (Amidon 2000, Fancy and Snetsinger 2001), partly because of the treacherous terrain, thick vegetation, and difficulty of working on Rota.

[1] Rota Avian Behavioral Ecology Program, Department of Psychology, University of Washington, P. O. Box 1298, Rota MP 96951, USA.

[2] Isa Consulting Services, P. O. Box 1381, Rota MP 96951, USA.

[3] Corresponding author; e-mail: lainieb@u.washington.edu

We searched the As Akoddo and Uyulan Hulo regions of Rota between 2003 and 2005. These regions occur on north-facing slopes with an elevation range of 150–400 m and are heavily forested with a dense cover of *Merrilliodendron megacarpum*. Eight active nests were found and monitored; six of these were filmed continuously until either the nestlings fledged or the nest failed. The nests were filmed using a black and white CCD infra-red camera placed 5–7 m from the nest, and recorded on a Sanyo SRT-2400DC real-time video cassette recorder. Our objectives were to examine nest fate and identify nest predators for possible future control measures.

OBSERVATIONS

All eight white-eye nests were in *Merrilliodendron megacarpum* trees. We observed nesting activity from March to July each year, although we also observed nest building in September. Four of the eight nests were successful in producing at least one fledgling. One nest was depredated by a Mariana Crow (*Corvus kubaryi*) during the nestling stage. One was depredated by a rat during the incubation stage, but this might have occurred after the nest was abandoned due to placement of the video camera too close to the nest (Thalia Sachtleben, pers. comm.). One nest failed because the eggs were cracked. The fate of the eighth nest was unknown. Clutch size was two eggs in all five nests for which clutch size was confirmed. The average number of fledglings from successful nests was 1.5 (n = 4).

DISCUSSION

All eight nests were in *Merrilliodendron megacarpum*, most likely because this was the predominant tree species in the area searched. Amidon et al. (2004) found Rota White-eye nests in four tree species (*Elaeocarpus joga*, *Hernandia labyrinthica*, *Merrilliodendron megacarpum*, and the introduced *Acacia con-*

fusa), but their study included searches in regions that were not dominated by *Merrilliodendron megacarpum*.

Amidon et al. (2004) observed active nests in December, March, July, and August, and reported indirect evidence of nesting in January, April, and June. Lusk and Taisacan (1997) reported a nesting season of at least March to June. In combination with our finding of nests between March and July and one instance of nest building in September, these observations suggest the Rota White-eye nesting season may extend as long as 10 months from December to September, and breeding may even occur year-round (Amidon et al. 2004).

Four of the eight nests monitored were successful in producing at least one fledgling. In comparison, seven of 10 nests monitored by Amidon et al. (2004) were successful in producing at least one fledgling; one was destroyed by a typhoon, one was depredated, and one was either depredated or abandoned, possibly due to human interference.

Sample sizes are small, but nest predation does not appear to be a significant factor affecting the reproductive success of Rota White-eyes in either the current study or in Amidon et al. (2004). The only species that was positively identified as a nest predator was the Mariana Crow, which is also endangered (USDI 1984); thus, control of this species is not possible. Introduced rats have caused population declines of birds on other Pacific islands (Atkinson 1977, King 1985), but nest predation by rats did not appear to be a significant cause of nest failure in this limited study. Sachtleben (2005) filmed nests of the Bridled White-eye (*Zosterops conspicillatus*), Golden White-eye (*Cleptornis marchei*), and Rufous Fantail (*Rhipidura rufifrons*) on Saipan, Northern Mariana Islands, and captured four predation events. Three nests were depredated by Micronesian Starlings (*Aplonis opaca*) and one by a Collared Kingfisher (*Todiramphus chloris*). Both species are native to Saipan and Rota. No nests were found to be depredated by rats, contrary to expectations (Sachtleben 2005). There was no evidence for nest predation by Black Drongos on Rota. Additional evidence on nest predator identity and the effects of nest predation on the breeding success of the Rota White-eye is required before predator control is initiated.

ACKNOWLEDGMENTS

We thank Shelly Kremer for encouragement and support of this work, Thalia Sachtleben for her insightful review of nest footage, Renee Ha for transferring video footage to DVD, and Monica Awasthy, Fred Amidon, and an anonymous reviewer for comments on the manuscript. This study was funded by a U.S. Fish and Wildlife Service Traditional Section 6 endangered species grant.

LITERATURE CITED

Amidon, F. A. 2000. Habitat relationships and life history of the Rota Bridled White-eye (*Zosterops rotensis*). Thesis. Virginia Polytechnic Institute and State University, Blacksburg, USA.

Amidon, F. A., C. A. Haas, and J. M. Morton. 2004. Breeding biology of the endangered Rota Bridled White-eye. Wilson Bulletin 116:342–346.

Atkinson, I. A. E. 1977. A reassessment of factors, particularly *Rattus rattus* L., that influenced the decline of endemic forest birds in the Hawaiian Islands. Pacific Science 31:109–133.

Craig, R. J. and E. Taisacan. 1994. Notes on the ecology and population decline of the Rota Bridled White-eye. Wilson Bulletin 106:165–169.

Engbring, J., F. L. Ramsey, and V. J. Wildman. 1986. Micronesian forest bird survey, 1982: Saipan, Tinian, Agiguan, and Rota. U.S. Fish and Wildlife Service, Honolulu, Hawaii, USA.

Fancy, S. G. and T. J. Snetsinger. 2001. What caused the decline of the Bridled White-eye on Rota, Mariana Islands? Studies in Avian Biology 22:274–280.

King, W. B. 1985. Island birds: will the future repeat the past? Pages 3–15 *in* Conservation of island birds (P. J. Moors, Editor). International Council for Bird Preservation Technical Publication Number 3. International Council for Bird Preservation, Cambridge, United Kingdom.

Lusk, M. R. and E. Taisacan. 1997. Description of a Bridled White-eye nest from Rota, Mariana Islands. Micronesica 30:183–185.

Sachtleben, T. 2005. Predation and nest success of forest birds in native and non-native habitat on Saipan, Mariana Islands. Thesis. Colorado State University, Fort Collins, USA.

U.S. Department of Interior (USDI). 1984. Endangered and threatened wildlife and plants; determination of endangered species status for seven birds and two bats of Guam and the Northern Mariana Islands; final rule. Federal Register 49: 33881–33885.

U.S. Department of Interior (USDI). 2004. Endangered and threatened wildlife and plants; endangered status for the Rota Bridled White-eye (*Zosterops rotensis*) from the Commonwealth of the Northern Mariana Islands; final rule. Federal Register 69:3022–3029.

The Wilson Journal of Ornithology 120(3):620–624, 2008

Predators at Nests of the Western Slaty Antshrike (*Thamnophilus atrinucha*)

Corey E. Tarwater[1,2]

ABSTRACT.—Predation is the primary cause of nest loss in most passerine species. While nest predation is important, the predator community and behaviors of parents and predators during predation events are poorly documented. I witnessed one and videotaped four predation events at nests of Western Slaty Antshrikes (*Thamnophilus atrinucha*) in central Panama. Predators included a snake (*Pseustes poecilonotus*), a monkey (white-faced capuchin [*Cebus capucinus*]), and three species of birds. Predators spent little time at the nest, yet some returned repeatedly to the same nest. Parents also returned several times to nests after the predation event and parental behaviors varied depending on the predator. Nest disturbance was not an accurate indicator of predator type. *Received 27 January 2007. Accepted 11 November 2007.*

Nest predation is the primary source of nest loss in most passerine species (Ricklefs 1969) and is likely a strong selective pressure in avian life histories (Martin 1996). Nest predation in tropical regions may be especially high and has been hypothesized to influence life history traits such as small clutch size and parental activity at the nest (Skutch 1985, Martin 1996). Most evidence of the identity of nest predators in the Neotropics is based on anecdotal or indirect evidence (Skutch 1985, Roper 1992, Sieving 1992, Robinson and Robinson 2001). A wide diversity of predators is typical of these forests (Ricklefs 1969, Skutch 1985, Sieving 1992) and studies suggest the importance of mammals (Roper 1992), snakes (Skutch 1985, Robinson et al. 2005a), and raptors (Skutch 1985, Robinson and Robinson 2001) in predation of bird nests. Identifying the predator community is important for understanding predator-prey interactions (Weatherhead and Bloun-Demers 2004), nest site selection (Weatherhead and Bloun-Demers 2004, Remes 2005), and evolution of parental care behaviors (Skutch 1949). Understanding parental behavior during predation events is necessary for examining whether parents accept risks to themselves by engaging in nest defense (Montgomerie and Weatherhead 1988, Pietz and Granfors 2005) and whether predator-specific responses occur (Montgomerie and Weatherhead 1988).

Direct observations of predation events are rare since the length of time predators spend at nests is often short. This results in low probability of the observer and the predator being at the nest at the same time (Robinson et al. 2005a). Identification of predators based on disturbance to the nest is also unreliable (Thompson et al. 1999, McCallum and Hannon 2001, Robinson et al. 2005a). Use of video cameras has become a popular and reliable tool for observing predation events (Thompson et al. 1999, Pietz and Granfors 2000, Robinson et al. 2005a) because of the challenges in identifying the predator community.

The objectives of this paper are to describe five predation events of nests of a neotropical passerine, the Western Slaty Antshrike (*Thamnophilus atrinucha*), and to evaluate the success of recording predation events by videotaping nests.

METHODS

I videotaped and monitored nests of Western Slaty Antshrikes in 2004–2006 in Parque Nacional Soberanía (mainland site) and Barro Colorado Island. Both sites are in lowland, tropical moist forests in the Republic of Panama (Karr 1971, Robinson 1999, Robinson et al. 2000). Most nests were found during building and were monitored every 2–3 days depending on stage. The incubation period is 16 days and the nestling period is 10 days

[1] Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, 606 East Healey Street, Champaign, IL 61820, USA.

[2] Current address: Program in Ecology, Evolution, and Conservation Biology, University of Illinois at Urbana-Champaign, 606 East Healey Street, Champaign, IL 61820, USA; e-mail: tarwater@uiuc.edu

(Skutch 1969, Oniki 1975, Robinson et al. 2000). The open cup nests of Slaty Antshrikes are in forks of trees and range from <1 m above ground to 6 m in height (Roper and Goldstein 1997).

Thirty-eight nests were videotaped of which 25 were filmed during the nestling period (24 nests in 2004). Video cameras (model: Sony CCD TRV 328) were placed 2–4 m from the nest (depending on the vegetation) in 2004 and nests were videotaped continuously from 0700 to1400 hrs (EST), except during heavy rain. Nests were filmed for 2–4 hr periods in 2006 (n = 7) and for shorter periods (<30 min) in 2005 (n = 7). Cameras were placed 10 m from the nest in 2005 and 2006 and nests were filmed throughout the day. I could not see nest defense by parents outside of a 1-m area around the nest, but vocalizations by parents could be heard at farther distances (~20 m). Camouflage and the surrounding vegetation were used in all years to minimize disturbance to the nest. Parents resumed apparently normal behavior after cameras were installed suggesting that disturbance to the nest was minimal.

RESULTS

Four predation events were filmed and one was observed. Three predation events filmed at the mainland site were by Double-toothed Kite (*Harpagus bidentatus*), Keel-billed Toucan (*Ramphastos sulfuratus*), and white-faced capuchin (*Cebus capucinus*). I also observed a Fasciated Antshrike (*Cymbilaimus lineatus*) prey on a nest at the mainland site. One predation event by a snake (*Pseustes poecilonotus*) was filmed on Barro Colorado Island.

Double-toothed Kite.—The antshrike nest was 2 m from the edge of the vegetation and 2 m above ground. The predation event occurred on day 7 of the nestling period. Videotaping of the nest (with 1 nestling) began at 0719 hrs. A Double-toothed Kite arrived at the nest at 0738 hrs. The kite pulled at the nestling and the nestling vocalized an apparent alarm sound. The kite bit at the nestling once again and departed after 1 min at the nest. An hour and 46 min later, another or the same Double-toothed Kite returned to the nest. The kite pecked at the nest for 1 min and then departed. A kite returned after 3 min, looked into the nest, and then flew away. Adult antshrikes were not heard vocalizing during predation or subsequent visits by the kite.

Each parent returned twice with prey following the predation event. The male arrived 24 min after predation, followed 30 min later by the female, and then the male 27 min later, and lastly the female after another 53 min (for a total of 140 min after predation). The parents did not return during the remaining 226 min of filming. The return intervals of parents to the nest were not unusually long as Slaty Antshrike parents provision young only a few times per hour. The adults called continuously each time they arrived with food. The parents, clearly disturbed, looked into and hopped in and out of the nest, and sang faintly. They then consumed the food item brought, and departed. Parents spent an average of 1.5 min at the nest. In addition to vocalizations at the nest, parents also called and sang faintly outside of the range of the video camera, but near the nest. Parents vocalized for about 3 min before returning to the nest and up to 5 min after leaving the nest.

Keel-billed Toucan.—The antshrike nest (with 2 nestlings) was far from any edge and 1 m in height above ground. The predation event occurred on day 7 of the nestling period. Filming of the nest began at 0719 hrs. The first indication of a disturbance was at 1330 hrs when one of the adults began alarm calling every 15 sec. Sounds of toucans flying overhead were heard at 1331 hrs and became louder as toucans approached the nest. The adult antshrikes were silent at 1333 hrs and movement was heard near the nest. A Keel-billed Toucan flew near the nest at 1334 hrs and hopped to a branch above the nest. The toucan took one of the nestlings without disturbing the nest. Both nestlings gave alarm calls during the event and one of the adults responded with alarm calls every 5 sec. One nestling fled the nest and fell to the ground while emitting alarm calls when the toucan took the first nestling. The toucan ate the nestling and left after spending <30 sec at the nest. Another or the same toucan returned to the nest 3 min later. Sounds of both the toucan and the remaining nestling were heard and then suddenly both were silent suggesting the toucan found the nestling. The adults continued to emit alarm calls for 18 min after the predation event at

which time the toucans were no longer heard in the video. The parents did not return to the nest during the remaining 38 min the nest was filmed after the predation event. The pair of antshrikes renested soon after the predation event confirming the loss of the second offspring.

White-faced Capuchin.—The antshrike nest (with 2 eggs) was on the edge of a small gap and 1.5 m above ground; the predation event occurred in the early stage of the incubation period. Filming of the nest began at 0830 hrs. The female antshrike was incubating for 2.5 hrs when white-faced capuchins were first heard on the tape (1101 hrs). Sounds of the monkeys became louder during the next 4 min. The incubating female began looking around more actively and left the nest at 1105 hrs. Soon (<30 sec later), the nest tree shook, followed 3 sec later with a monkey in view. The monkey lowered the nest branch from the ground and reached into the nest to take the eggs, breaking the branch in the process. The monkey preyed on the nest and left the video within 10 sec of arrival. Monkeys were heard in the video for an additional 8 min. The parents began calling at 3–5 sec intervals 9 min (1123 hrs) after the monkeys were no longer heard in the video. Their alarm calls got louder in the video as they approached the nest. The male arrived at the nest at 1136 hrs, looked into the nest, and called three times. He departed after 1 min, while calling. Alarm calls continued becoming quieter as the pair moved away from the nest until 1140 hrs, when no further vocalizations were heard. Nothing else noteworthy happened during the remaining 57 min the nest was filmed.

Fasciated Antshrike.—This predation event occurred in the early stage of the incubation period. The nest had two eggs and was in the middle of a small gap at a height of 3.5 m above ground. I was nearby at 1400 hrs when I heard the Slaty Antshrike alarm call. I arrived at the nest and saw a male Fasciated Antshrike pecking at eggs in the nest. The male and female Slaty Antshrikes were calling and flying back and forth, 0.5–2 m from the nest. The male Slaty Antshrike attacked the male Fasciated Antshrike, striking him three times. The Fasciated Antshrike would leave the nest after each attack, but would return within a few seconds. Once the male Fasciated Antshrike finished at the nest, the Fasciated Antshrike pair left the vicinity of the Slaty Antshrike nest and vocalized for the next minute. The female Fasciated Antshrike stayed within the vicinity of the nest while the male preyed upon the eggs, but was not part of the predation event. The Slaty Antshrikes called while the Fasciated Antshrikes were in the area. The male Slaty Antshrike returned to the nest <1 min after the predation event occurred, pecked into the nest 3–4 times, and then flew away. I did not continue observing the nest after the male departed.

Pseustes poecilanotus.—This nest (with 1 nestling) was far from an edge and 1.25 m in height above ground. The predation event occurred on day 2 of the nestling period. I flushed the female from the nest just prior to videotaping the nest (filming began at 0804 hrs). Both parents subsequently vocalized, but when filming began, they were >20 m from the nest and silent. The snake came into view at 0811 hrs. The snake was at the nest for 2 min while swallowing the nestling. The parents were not heard vocalizing during predation of the nestling. The female returned 25 min after the snake had departed and sat on the empty nest for 61 min. The male arrived with food a few seconds after the female departed. The male vocalized (faint songs and contact calls), hopped around the nest, ate the food item, and then departed after 3 min. The nest was filmed for an additional 158 min during which time neither birds nor snake returned.

Success of Recording Predation Events by Videotaping Nests.—Four hundred and seventeen hrs of observations were filmed (n = 38 nests) of which 397 hrs were from 24 nests during the nestling period. Twenty-three of 38 nests that were filmed were depredated (60.5%). Of 354 nests that were not filmed, 281 (79.4%) were lost due to predation. The difference in percent nests lost was likely because most nests were filmed during the nestling period. A greater number of nests were depredated during incubation (252 of 304 total predation events occurred during the incubation period). The number of predation events recorded (of the total number of hours nests were filmed) was 0.01 predation events/hr filmed.

DISCUSSION

Keel-billed Toucans, *Pseustes*, Double-toothed Kites, and white-faced capuchins have been observed preying on bird nests (Willis 1972, Skutch 1985, Robinson and Robinson 2001, Robinson et al. 2005a). This is the first observation of a Fasciated Antshrike as a nest predator. Slaty and Fasciated antshrikes are commonly sympatric, often attending understory antwren flocks together. However, when Slaty Antshrikes have a nest or young fledglings, the parents call and displace Fasciated Antshrikes when they approach their offspring. This suggests that Fasciated Antshrikes are perceived by Slaty Antshrikes as a threat.

The behaviors of the predators during the predation events were similar to other observations of predators at nests. Predators may return repeatedly to the nest (Marzluff 1985, Stake and Cimprich 2003, Stake et al. 2004) and spend little time at nests (Robinson et al. 2005a). Predators at antshrike nests did not spend more than 2 min at a nest. Additionally, features of nest disturbance do not provide reliable information to identify predators (Thompson et al. 1999; McCallum and Hannon 2001; Robinson et al. 2005a, b). Predation due to mammals is often associated with nest disturbance and predation by birds is not. However, both the Double-toothed Kite and the white-faced capuchin damaged the nest in this study. The toucan, Fasciated Antshrike, and snake left no evidence that might identify the predator.

Parental defense behavior can vary depending upon the risk the predator poses and likelihood of successfully defending the nest (Montgomerie and Weatherhead 1988, Ghalambor and Martin 2001). Toucans and Fasciated Antshrikes are probably not threats to an adult Slaty Antshrike, whereas a Double-toothed Kite might be (Willis 1972). The Slaty Antshrike pair vocalized during and after the predation event by the toucan, and adults were aggressive in their nest defense with the Fasciated Antshrike. Fasciated and Slaty antshrikes are similar in size. The parents may have been willing to attack the predator because of the small threat to themselves and greater probability of successfully defending the nest. However, in the case of the Double-toothed Kite(s), the parents did not vocalize when this species was at the nest. The parents potentially remained silent when the kite(s) was present to reduce their risk. The parents were silent while monkeys were close to their nest. It is unlikely that a capuchin could prey on an adult off the nest, but vocalizations by parents are also unlikely to deter monkeys.

Adults returned to nests after predation events. Although attendance of empty nests may occur, (Pietz and Granfors 2000; M. M. Libsch and CET, pers. obs.), the phenomena is rarely reported. Despite high predation of Slaty Antshrike nests, few predation events were observed on videotape. More filming during the highest mortality period of the nesting cycle is required to record a greater number of predation events. A diversity of predators exists in the lowland forests of Panama and parental behavior varies depending on species of predator. More work is needed to understand the importance of the different predators on nest success and to identify the predator community.

ACKNOWLEDGMENTS

I thank S. K. and R. D. Bassar, C. G. Batista, B. M. Hancock, B. G. Lascelles, M. G. Meadows, and I. R. Ochoa for help collecting the field data that made this study possible. I also thank J. P. Kelley and M. M. Libsch for support and the Smithsonian Tropical Research Institute for logistical support. I thank J. D. Brawn, P. J. Weatherhead, and A.V. Suarez for helpful comments on the manuscript. This work was funded by National Science Foundation grant IBN-0212587 and grants from the University of Illinois.

LITERATURE CITED

Ghalambor, C. K. and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494–497.

Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecological Monographs 41:207–233.

Martin, T. E. 1996. Life-history evolution in tropical and south temperate birds: what do we really know? Journal of Avian Biology 27:263–272.

Marzluff, J. M. 1985. Behavior at a Pinyon Jay nest in response to predation. Condor 87:559–561.

McCallum, C. A. and S. J. Hannon. 2001. Accipiter predation of American Redstart nestlings. Condor 103:192–194.

Montgomerie, R. D. and P. J. Weatherhead. 1988. Risks and rewards of nest defense by parent birds. Quarterly Review of Biology 63:167–187.

Oniki, Y. 1975. The behavior and ecology of Slaty

Antshrikes (*Thamnophilus punctatus*) on Barro Colorado Island, Panama Canal Zone. Annals de Academia Brasil Ciencias 47:471–515.

Pietz, P. J. and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64:71–87.

Pietz, P. J. and D. A. Granfors. 2005. Parental nest defense on videotape: more reality than "myth." Auk 122:701–705.

Remes, V. 2005. Birds and rodents destroy different nests: a study of Blackcap *Sylvia atricapilla* using the removal of nest concealment. Ibis 147:213–216.

Ricklefs, R. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

Robinson, W. D. 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. Conservation Biology 13:85–97.

Robinson, W. D. and T. R. Robinson. 2001. Observations of predation events at bird nests in central Panama. Journal of Field Ornithology 72:43–48.

Robinson, W. D., G. Rompre, and T. R. Robinson. 2005a. Videography of Panama bird nests shows snakes are principal predators. Ornithologia Neotropical 16:187–195.

Robinson, W. D., J. N. Styrsky, and J. D. Brawn. 2005b. Are artificial bird nests effective surrogates for estimating predation on real bird nests? A test with tropical birds. Auk 122:843–852.

Robinson, W., T. Robinson, S. Robinson, and J. Brawn. 2000. Nesting success of understory forest birds in central Panama. Journal of Avian Biology 31:151–164.

Roper, J. J. 1992. Nest predation experiments with quail eggs—too much to swallow. Oikos 65:528–530.

Roper, J. J. and R. R. Goldstein. 1997. A test of the Skutch hypothesis: does activity at nests increase nest predation risk? Journal of Avian Biology 28: 111–116.

Sieving, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of central Panama. Ecology 73:2310–2328.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

Skutch, A. F. 1969. Life histories of Central American birds. III. Pacific Coast Avifauna 35:172–179.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Ornithological Monographs 36:575–594.

Stake, M. M. and D. A. Cimprich. 2003. Using video to monitor predation at Black-capped Vireo nests. Condor 105:348–357.

Stake, M. M., J. Faaborg, and F. R. Thompson. 2004. Video identification of predators at Golden-cheeked Warbler nests. Journal of Field Ornithology 75:337–344.

Thompson, F. R., W. Dijak, and D. E. Burhans. 1999. Video identification of predators at songbird nests in old fields. Auk 116:259–264.

Weatherhead, P. J. and G. Bloun-Demers. 2004. Understanding avian nest predation: why ornithologists should study snakes. Journal of Avian Biology 35:185–190.

Willis, E. O. 1972. The behavior of Spotted Antbirds. Ornithological Monographs 10.

The Wilson Journal of Ornithology 120(3):625–627, 2008

Evidence for Bachman's Sparrow Raising Brown-headed Cowbirds to Fledging

Matthew J. Reetz,[1,4] Elizabeth Farley,[2] and Thomas A. Contreras[3]

ABSTRACT.—We report the first records of Brown-headed Cowbirds (*Molothrus ater*) raised to fledging by Bachman's Sparrow (*Aimophila aestivalis*). Records are based on field observations of parasitized sparrow nests monitored during two separate avian reproductive studies. One record is of a Bachman's Sparrow nest in southwestern Florida in 2002 and four records are of unpublished data from sparrow nests in central Arkansas during 1983–1985. These observations suggest that Bachman's Sparrow can successfully raise cowbird young. Ours is also the first record of a parasitized Bachman's Sparrow nest in Florida. *Received 5 October 2007. Accepted 16 January 2008.*

Bachman's Sparrow (*Aimophila aestivalis*) is a resident of pine (*Pinus* spp.) flatwoods, grasslands, and dry prairies of the southeastern United States. It ranges from southern Florida to southern Virginia and west to eastern Texas (Dunning 1993). The range of Bachman's Sparrow receded after an initial increase in distribution and abundance around the turn of the 20th century (Bent 1968), and populations have shown a >50% decrease during 1966–2006 (Sauer et al. 2006). Habitat loss and degradation are the most significant threats to Bachman's Sparrow populations, but the expansion of the Brown-headed Cowbird (*Molothrus ater*) into the southeastern United States may negatively impact host populations that lack historical exposure to parasitism.

Nests of Bachman's Sparrow are infrequently found to be parasitized by the Brown-headed Cowbird (Dunning 1993). Brown-headed Cowbirds are known to parasitize >220 species, yet more than a third of parasitized species are not known to raise cowbird young (reviewed in Ortega 1998, Rasmussen and Sealy 2006). We found no instances in the literature of a Bachman's Sparrow raising a cowbird to fledging or feeding a cowbird fledgling outside of the nest and only one where a Bachman's Sparrow nest contained a cowbird nestling (Haggerty 1988). We present evidence for the first known instances of Brown-headed Cowbirds successfully fledging from nests of Bachman's Sparrow.

METHODS

We monitored avian productivity at Myakka River State Park (MRSP) in southwest Florida (27° 12′ N, 82° 15′ W) from April to August 2000–2004. MRSP is 11,800 ha of primarily dry prairie and flatwood habitats characterized by an understory of herbaceous ground cover and saw palmetto (*Serenoa repens*) with a canopy of scattered longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*), live oak (*Quercus virginiana*), and sabal palm (*Sabal palmetto*). Prescribed fire programs at MRSP were initiated in the mid-1970s to restore natural characteristics of fire-dependent habitats, including those occupied by Bachman's Sparrows, which are year-round residents.

OBSERVATIONS

We monitored 285 nests of 25 breeding bird species in MRSP from 2000 to 2004. Ten nests were from at least nine Bachman Sparrow pairs. One nest was discovered on 9 June 2002 when the female flushed from the nest which was on the ground and hidden beneath two saw palmetto fronds. The nest contained three pinkish-white sparrow eggs and one speckled cowbird egg. The nest contents were photographed following discovery to confirm identification of the cowbird egg. We assume the egg was of a Brown-headed Cowbird and

[1] Department of Wildlife Ecology and Conservation, University of Florida, P. O. Box 110430, Gainesville, FL 32611, USA.

[2] Department of Biology, University of Texas at Tyler, 3900 University Boulevard, Tyler, TX 75799, USA.

[3] Department of Biology, Washington and Jefferson College, 60 South Lincoln Street, Washington, PA 15301, USA.

[4] Corresponding author; e-mail: aves@ufl.edu

not a Shiny Cowbird (*Molothrus bonariensis*) which has not been confirmed breeding in North America.

The nest was monitored every 2–4 days and on 21 June was found to contain three nestlings (i.e., 1 cowbird, 2 sparrows) and one cracked sparrow egg. The cowbird nestling was slightly larger than the two sparrow nestlings indicating that it likely hatched on 19–20 June while the sparrow nestlings hatched on 20–21 June. The three nestlings were in apparent good health and begged on subsequent nest-checks. All nestlings were large and well-feathered on 29 June with the cowbird nestling being slightly larger than the sparrows. All birds appeared to be within 1–3 days of fledging from the nest. The nest was last checked on 2 July and was empty and showed no signs of disturbance. Two adult sparrows were chipping nearby and at least one sparrow young was heard calling from nearby vegetation. We estimate that all nestlings fledged between 30 June and 1 July but the cowbird likely fledged earlier than the sparrow nestlings. We were not able to locate the cowbird fledgling outside of the nest, possibly due to the presence of dense vegetation where fledglings could be hidden. We assume the cowbird fledged from the nest because there was no evidence that it or any of the sparrow young did not fledge.

Haggerty (1988) monitored 66 Bachman's Sparrow nests in Hot Spring County, Arkansas (34° 11′ N, 92° 48′ W) from May to August 1983–1985. Sites primarily consisted of shortleaf (*Pinus echinada*) and loblolly pine (*P. taeda*) plantations. With the author's permission, we present observations of all four parasitized Bachman's Sparrow nests, two of which likely fledged cowbird young. Nest #6 was found with one cowbird egg and three Bachman's Sparrow eggs. All eggs hatched but the nest was depredated on day 5 of the nestling period. Nest #61 was found with three sparrow eggs and one cowbird egg. The cowbird egg and two sparrow eggs hatched. The nest was depredated on about day 7 of the nestling period. Nest #35 was found with a single cowbird egg and four Bachman's Sparrow eggs. Three sparrow eggs disappeared during the laying period and the first few days of incubation, one of which was found pierced on the ground near the nest. Both the remaining sparrow egg and cowbird egg hatched and both nestlings fledged on day 9 of the nestling period. They were not observed again in the adult territory. Nest #60 was found on day 4 or 5 of the nestling period based on the size of a recently dead sparrow nestling. The two nestlings remaining in the nest were both cowbirds of similar age. The fate of this nest is not known.

DISCUSSION

Reports of cowbird parasitism of Bachman's Sparrow nests are rare. Friedmann (1963) notes only three records of parasitism, one each from Kentucky, Missouri, and West Virginia. No cases of parasitism were reported in 34 Bachman's Sparrow nests in Alabama (Tucker et al. 2006) and 56 nests monitored during three studies in Georgia and South Carolina (reviewed by Kilgo and Moorman 2003). Perkins et al. (2003) did not report cowbird parasitism in any of the 40 nests of Bachman's Sparrow they monitored in central Florida. Congeneric Botteri's (*Aimophila botterii*), Rufous-crowned (*A. ruficeps*), and Cassin's sparrows (*A. cassinii*) are also infrequently parasitized (Webb and Bock 1993, Collins 1999, Dunning et al. 1999), while Five-striped (*A. quinquestriata*) and Rufous-winged sparrows (*A. carpalis*) have low to intermediate parasitism rates (Groschupf 1992, Lowther et al. 1999). Rufous-winged, Rufous-crowned, and Five-striped sparrows each have been reported to successfully raise a cowbird or have been seen feeding a cowbird fledgling (Ohmart 1969, Mills et al. 1980, Miles 1986). Our observations represent the first evidence of Bachman's Sparrow successfully fledging cowbird young. Furthermore, our records are the first to document successful hatching of cowbird eggs or nests found with cowbird nestlings. To our knowledge, this is also the first reported case of cowbird parasitism of Bachman's Sparrow in Florida.

ACKNOWLEDGMENTS

We thank T. M. Haggerty for access to nest records from central Arkansas and permission to publish observations of cowbird parasitism. We thank the managers and staff at Myakka River State Park and K. W. Outcalt (USDA Southern Research Station) for logistical support and access to field sites. Invaluable field assistance was provided by M. D. Alderman, G. S. Kaufmann, and E. S. Owens. We thank K. E. Sieving

for support and help with field protocols. This is Contribution Number 175 of the National Fire and Fire Surrogate Project (FFS) funded by the U.S. Joint Fire Science Program. Protocols were approved under University of Florida IACUC #A530.

LITERATURE CITED

Bent, A. C. 1968. Life Histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. National Museum Bulletin 237, Part 2.

Collins, P. W. 1999. Rufous-crowned Sparrow (*Aimophila ruficeps*). The birds of North America. Number 472.

Dunning, J. B. 1993. Bachman's Sparrow (*Aimophila aestivalis*). The birds of North America. Number 38.

Dunning Jr., J. B., R. K. Bowers Jr., S. J. Suter, and C. E. Bock. 1999. Cassin's Sparrow (*Aimophila cassinii*). The birds of North America. Number 471.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. National Museum Bulletin 233.

Groschupf, K. 1992. Five-striped Sparrow (*Aimophila quinquestriata*). The birds of North America. Number 21.

Haggerty, T. M. 1988. Aspects of the breeding biology and productivity of Bachman's Sparrow in central Arkansas. Wilson Bulletin 100:247–255.

Kilgo, J. C. and C. E. Moorman. 2003. Patterns of cowbird parasitism in the southern Atlantic Coastal Plain and Piedmont. Wilson Bulletin 115:277–284.

Lowther, P. E., K. D. Groschupf, and S. M. Russell. 1999. Rufous-winged Sparrow (*Aimophila carpalis*). The birds of North America. Number 422.

Miles, D. B. 1986. A record of Brown-headed Cowbird (*Molothrus ater*) nest parasitism of Rufous-crowned Sparrows (*Aimophila ruficeps*). Southwestern Naturalist 51:253–254.

Mills, S., J. Silliman, K. Groschupf, and S. Speich. 1980. Life history of the Five-striped Sparrow. Living Bird 18:95–110.

Ohmart, R. D. 1969. Physiological and ethological adaptations of the Rufous-winged Sparrow (*Aimophila carpalis*) to a desert environment. Dissertation. University of Arizona, Tucson, USA.

Ortega, C. P. 1998. Cowbirds and other brood parasites. University of Arizona Press, Tucson, USA.

Perkins, D. W., P. D. Vickery, and W. G. Shriver. 2003. Spatial dynamics of source-sink habitats: effects on rare grassland birds. Journal of Wildlife Management 67:588–599.

Rasmussen, J. L. and S. G. Sealy. 2006. Hosts feeding only Brown-headed Cowbird fledglings: where are the host fledglings? Journal of Field Ornithology 77:269–279.

Sauer, J. R., J. E. Hines, and J. Fallon. 2006. The North American Breeding Bird Survey, results and analysis 1966–2005. Version 6.2.2006. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. http://www.mbr-pwrc.usgs.gov/bbs/bbs.html (accessed 11 September 2007).

Tucker Jr., J. W., W. D. Robinson, and J. B. Grand. 2006. Breeding productivity of Bachman's Sparrows in fire-managed longleaf pine forests. Wilson Journal of Ornithology 118:131–137.

Webb, E. A. and C. E. Bock. 1993. Botteri's Sparrow (*Aimophila botterii*). The birds of North America. Number 216.

The Wilson Journal of Ornithology 120(3):628–630, 2008

Simultaneous Incubation by Two Females and Nestling Provisioning by Four Adults at a Savannah Sparrow Nest

Nathan J. Zalik[1] and Noah G. Perlut[1,2,3]

ABSTRACT.—We present the first observations of misdirected parental care by Savannah Sparrows (*Passerculus sandwichensis*) including a rare occurrence of simultaneous incubation. Two females simultaneously incubated eggs, brooded, and fed nestlings, and two males fed nestlings in one nest. These behaviors may have been prompted by strong parental instincts in combination with a stressful breeding environment mediated by hayfield management, as any genetic benefits were unlikely. *Received 1 September 2007. Accepted 24 October 2007.*

Cooperative breeding, in which care for young is provided by individuals other than the breeding pair, is estimated to occur in only 9% of avian species (Cockburn 2006). Cooperative breeding is thought to evolve when the additional help allows for greater production of young or increased survival of adults through reduced breeding effort (Brown 1978, Crick 1992). Helpers may receive resource benefits from being a member of a group or may enhance future breeding opportunities. Furthermore, helpers that are closely related to the breeders they assist gain indirect genetic benefits from raising kin (Hamilton 1963, 1964). Alternatively, Jamieson (1986, 1991) hypothesized that helping is a behavioral response to the presence of begging young. This "misdirected parental care" (Price et al. 1983: 192) may explain rare cases of feeding or incubation by individuals which do not appear to receive resource or genetic benefits.

Avian incubation is usually performed by only one individual at any given time regardless of the parental care system. Incubation and brooding by more than one bird simultaneously has rarely been documented for temperate species (Forbush 1929, Howell 1942, Bellrose 1943, Hawksley and McCormack 1951, Brackbill 1952, Fuller and Bolen 1963). We present observations of misdirected parental care by the Savannah Sparrow (*Passerculus sandwichensis*), a ground-nesting songbird with a mixed-mating strategy and biparental care (Wheelwright and Rising 1993). We describe simultaneous incubation, brooding, and provisioning of young by two females, and provisioning young by two males.

METHODS

We captured and uniquely banded (U.S. Geological Survey [USGS] metal band and three colored leg bands) all breeding adult Savannah Sparrows in 2002–2007 on a 10.5-ha managed hayfield (44° 39′ N, 73° 27′ W) in Shelburne, Vermont, USA. We located Savannah Sparrow nests (n = 515) and monitored them every 1–3 days until they fledged or failed, and banded nestlings (USGS band only) on post-hatch day 6–7 (Perlut et al. 2006).

OBSERVATIONS

On 12 July 2007 we found a nest containing four eggs being incubated by a female Savannah Sparrow with two orange bands on the left leg and a yellow and metal band on the right leg (hereafter referred to as the primary female). On the same day, we discovered another nest containing four eggs being incubated by a female with metal and blue bands on the left leg and orange and red bands on the right leg (hereafter referred to as the secondary female). These nests, 73 m apart, were on adjacent territories. Both females were still incubating four eggs on 13 July. By 16 July, the secondary female's nest had failed, while the primary female was still incubating four eggs. On 17 July, two birds flushed ~0.5 m from each other from the area of the primary female's nest. One of these birds was identi-

[1] The Rubenstein School of Environment and Natural Resources, 81 Carrigan Drive, University of Vermont, Burlington, VT 05405, USA.

[2] Vermont Cooperative Fish and Wildlife Research Unit, 81 Carrigan Drive, University of Vermont, Burlington, VT 05405, USA.

[3] Corresponding author; e-mail: nperlut@uvm.edu

fied as the secondary female. The secondary female's nest had recently failed and no further attempts to follow this bird were made as it was too soon for her to have renested. On 20 July, two birds flushed directly from the primary female's nest. The rim of the nest was flattened on one side, making the nest cup atypically wide. Within minutes, both primary and secondary females returned to the nest. We flushed the birds two more times to reconfirm these observations, flushing from within 1 m of each other and directly from the nest together. We searched the area extensively for a second nest, but none was located.

On 20 July, at 1000 hrs EDT the nest had four eggs, one of which appeared damaged with a small indentation. We videotaped the nest using a small (9 × 3 × 3 cm) wide angle lens at 1325 hrs, at which time the nest contained one nestling and three unhatched eggs. We made two recordings, one of 30 min and one of 17 min; both females were observed incubating simultaneously as well as singly. They sat together on the nest for 11 min during one period with the primary female in a normal incubating posture and the secondary female sitting partially on the back of the primary female and partially on the rim of the nest. Both birds were facing roughly the same direction. This simultaneous incubation ended when we approached the nest to remove the camera. On six occasions a bird forced itself underneath the other already incubating bird to begin incubating the nest itself. During one 22-sec period, this forceful exchange occurred three times.

We recorded (4.5 hrs) the nestling stage at post-hatch 4–5 days. Additional aggressive behavior between the two females beyond the forceful incubation exchanges occurred. When a female was on the nest and the other female approached, it would often do so with one or both wings raised and give aggressive squealing and chattering calls. During one interaction, while the primary female was brooding, the secondary female arrived at the nest with both wings raised and made a squealing vocalization. The two birds faced each other with bills agape for 1 min as the primary female remained on the nest. The interaction ended when the primary female pecked at the secondary female, causing the secondary female to retreat. These vocalizations and displays were notably different from those observed when one female and one male interacted at the nest. Despite these aggressive interactions, the primary female tolerated the secondary female, as evidenced by simultaneous incubation, brooding, and provisioning of young.

Two of the four eggs hatched and the two damaged or infertile eggs were removed by 23 July. Both females continued to brood and provision the nestlings. Two males also were observed provisioning nestlings. The male which frequently brought food was the social male associated with the primary female's two previous nesting attempts. The second male was the social male associated with the secondary female's previous nesting attempts. This second male visited the nest and fed nestlings only once during the recordings. The nestlings fledged on 29 July.

DISCUSSION

Our observations represent the first documented case of misdirected parental care occurring naturally at a Savannah Sparrow nest. Weatherhead and Robertson (1978, 1980) describe a case of helping induced artificially and a second case where clutches were laid simultaneously by two females in the same nest. Why did the secondary female (and her mate) help at the nest rather than initiate another nesting attempt? We have no reason to suspect intraspecific brood parasitism, as both females had active nests simultaneously, and the number of eggs in the primary female's nest remained at four throughout the incubation period. Paternity assignment of 109 broods in a related study revealed no evidence of egg dumping (N. G. Perlut, unpubl. data); Savannah Sparrows on Kent Island, New Brunswick show no evidence of egg dumping (C. R. Freeman-Gallant, pers. comm.). We do not know whether the two birds were related, as both were first banded as adults on 15 May 2007. It seems improbable the secondary female had any direct genetic investment in the nest despite this uncertainty.

We suspect the secondary female discovered the primary female's nest while foraging and her maternal instinct was to incubate the eggs. Females likely monitor the breeding status of their neighbors, as the field is densely populated (2 females/ha in 2007) and individuals commonly interact. Other females at this site initiated renests around the date the nest of the secondary

female failed; some females have laid up to six clutches in a year, fledging as late as 24 August. Thus, there were sufficient resources and time with which to renest. The sight of eggs in a nest may have stimulated hormones that led to an incubation response. This effect was perhaps similar to the response of adults to nestlings of brood parasites, in which parental instincts and mistaken identity cause a maladaptive response to feed nestlings (Price et al. 1983). Similarly, the secondary male likely provisioned young simply because his mate was caring for the nest.

Stress, mediated by the effects of hayfield management, likely contributed to this unusual behavior. The secondary female had attempted three previous nests. The field was cut twice during the nesting season, each cutting followed by manure application; all active nests failed as a result of haying. These sources of nest failure, in addition to failure from natural causes, may have placed these birds under high stress. It is possible these factors contributed to the secondary female's "decision" to attend this nest rather than initiate another clutch.

The secondary female and her mate assisted in incubation and in provisioning nestlings. However, whether these birds helped rather than hindered development of the young is debatable. For instance, only two young reached the fledgling stage, whereas the average number of fledged young from successful post-second harvest nests was 3.0 (n = 10) in 2007. Of the two young that survived, one nestling's leg was splayed to the side. This could have been a genetic defect, but was more likely an injury sustained in the nest, possibly during an interaction between the two females.

Our observations of simultaneous incubation and provisioning of young by Savannah Sparrows are highly unusual and may have been prompted by misguided parental instincts in combination with a stressful breeding environment.

ACKNOWLEDGMENTS

This project was supported by The Rubenstein School of Environment and Natural Resources, University of Vermont, as well as the Initiative for Future Agricultural and Food Systems, and the National Research Initiative of the USDA, Cooperative State Research, Education and Extension Service, grant numbers 2001-52103-11351 and 03-35101-13817, respectively. We thank Shelburne Farms and Sam Dixon for access to their land, and Allan Strong, James Rising, and Patrick Weatherhead for helpful comments on the manuscript.

LITERATURE CITED

Bellrose Jr., F. 1943. Two Wood Ducks incubating in the same nesting box. Auk 60:446–447.

Brackbill, H. 1952. A joint nesting of Cardinals and Song Sparrows. Auk 69:302–307.

Brown, J. L. 1978. Avian communal breeding systems. Annual Review of Ecology and Systematics 9:123–155.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. Proceedings of the Royal Society B-Biological Sciences 273:1375–1383.

Crick, H. P. Q. 1992. Load-lightening in cooperatively breeding birds and the cost of reproduction. Ibis 134:56–61.

Forbush, E. H. 1929. Birds of Massachusetts and other New England states. Volume 3. Berwick and Smith Company, Norwood, Massachusetts, USA.

Fuller, R. W. and E. Bolen. 1963. Dual Wood Duck occupancy of a nest box. Wilson Bulletin 75:94–95.

Hamilton, W. D. 1963. The evolution of altruistic behavior. American Naturalist 97:354–356.

Hamilton, W. D. 1964. The genetical evolution of social behavior, I and II. Journal of Theoretical Biology 7:1–52.

Hawksley, O. and A. P. McCormack. 1951. Doubly occupied nests of the Eastern Cardinal *Richmondena cardinalis*. Auk 68:515–516.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin (*Turdus migratorius* L.). American Midland Naturalist 28:529–603.

Jamieson, I. G. 1986. The functional approach to behavior: is it useful? American Naturalist 127:195–208.

Jamieson, I. G. 1991. The unselected hypothesis for the evolution of helping behavior: too much or too little emphasis on natural selection? American Naturalist 138:271–282.

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. Ecological Applications 16:2235–2247.

Price, T., S. Millington, and P. Grant. 1983. Helping at the nest in Darwin's Finches as misdirected parental care. Auk 100:192–194.

Weatherhead, P. J. and R. J. Robertson. 1978. Intraspecific nest parasitism in the Savannah Sparrow. Auk 95:744–745.

Weatherhead, P. J. and R. J. Robertson. 1980. Altruism in the Savannah Sparrow? Behavioral Ecology and Sociobiology 6:185–186.

Wheelwright, N. T. and J. D. Rising. 1993. Savannah Sparrow (*Passerculus sandwichensis*). The birds of North America. Number 45.

The Wilson Journal of Ornithology 120(3):631–632, 2008

Grey Heron (*Ardea cinerea*) Predation on the Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus*)

Pierre A. Pistorius[1]

ABSTRACT.—Grey Herons (*Ardea cinerea*) typically prey upon fish and other aquatic organisms with occasional reports of predating small birds. I report observations of one or more Grey Herons predating on Aldabra White-throated Rails (*Dryolimnas cuvieri aldabranus*) on Picard Island (Aldabra Atoll, Seychelles). Grey Herons were observed on two occasions having caught rails and, on another occasion, a heron was observed ambushing and pursuing rails with no success. Heron(s) were not observed ingesting the rails, as they flew or ran off with their prey, but it is likely the rails were consumed. These are the first observations of any form of predation on the Aldabra White-throated Rail, which is one of the largest recorded avian prey of the Grey Heron. *Received 25 June 2007. Accepted 1 November 2007.*

The Grey Heron (*Ardea cinerea*), widespread throughout the Seychelles, is one of the few waders that breed on Aldabra Atoll (9° 24′ S, 46° 20′ E) (Feare and Watson 1984). The Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus*) is endemic to Aldabra and represents the last remaining flightless bird in the Indian Ocean. It is believed the White-throated Rail lost the ability to fly on Aldabra due to lack of predatory pressure on the atoll (Wanless 2003). There are wild cats (*Felis silvestris*) on the largest of the four islands (Grand Terre) making up the atoll; rails occur only on the three islands which are cat-free. Rails were reintroduced to Picard Island in 1999 (Wanless 2002, Wanless et al. 2002). Rails tend to flee on sight of a large bird (e.g., heron or crow), possibly an instinct retained from their distant past, and it has been noted there are no birds on Aldabra sufficiently large to kill adult Aldabra Rails (Wanless 2002).

OBSERVATIONS

Grey Herons were observed predating on White-throated Rails on 14 June 2007 at 1430 hrs (GMT + 0400) and again on 21 June at 1615 hrs. The first event occurred on the beach and the second in an open area close to shrub vegetation on Picard Island when attention was drawn to the events by loud vocalization by the rails. Observations were made with the naked eye from distances between 20 and 30 m. On the first occasion, an adult Grey Heron was seen with a rail of unknown age in its beak. When approached by the observer, it rushed into the shrub vegetation carrying the rail with it. The rail was still alive at last sight and it is not known how events proceeded. On the second occasion, a Grey Heron was seen holding an adult rail with one foot and pecking vigorously at the still alive rail. It then flew with the rail in its beak. Further to these observations, on 25 June at 1030 hrs an adult Grey Heron was seen ambushing and pursuing a juvenile rail with no success. All three incidents reported occurred in the same area and it is likely the same individual heron was involved each time.

DISCUSSION

Grey Herons generally target aquatic prey, mostly fish, but have been reported to feed on small mammals, invertebrates, and occasionally on other birds (Marquiss and Leitch 1990, McCanch 2003, Jakubas and Mioduszewska 2005, Gwiazda and Amirowicz 2006, Williams and Ward 2006). Avian prey of Grey Heron is usually relatively small, e.g., Common Moorhen (*Gallinula chloropus*) chicks, young Mallard (*Anas platyrhynchos*) and Tufted Duck (*Aythya fuligula*) ducklings, and Cape Cormorant (*Leucocarbo capensis*) chicks (Milstein et al. 1970, Marquiss and Leitch 1990, Williams and Ward 2006). Attempts of hunting for larger birds have been reported occasionally. McCanch (2003) described a Grey Heron that choked to death while trying to ingest a Little Grebe (*Tachybaptus ruficollis*). Adult Little Grebes weigh

[1] Seychelles Island Foundation, Mont Fleuri, P. O. Box 853, Victoria, Mahe, Seychelles; e-mail: ppistorius@zoology.up.ac.za

~140 g (Ogilvie 2003) compared to Aldabra White-throated Rails that weigh ~180 g (Wanless 2003). During the time of the reported observations, juvenile Aldabra rails would have been about 6 months of age and of similar weight to the adults. The fate of the two rails that were caught (nor the heron) could not be ascertained. A rail with a broken wing was last seen in the study area during the period when the predation was observed, and may have been hunted by the heron. That a heron was observed spending several hours hunting for rails suggests rails have successfully been captured and consumed, and form a rewarding target species.

Population growth of Aldabra White-throated Rails during the first 2 years after the introduction of rails to Picard Island was exponential and it was estimated the population would reach carrying capacity between 2007 and 2009 (Wanless 2002). Recent observations of large numbers of rails injured in territorial disputes and juveniles remaining in adult territories (pers. obs.) suggest that carrying capacity may have been reached. Individual rails are also often observed feeding in the inter-tidal zone, behavior which is generally uncommon in the Aldabra White-throated Rail (Penny and Diamond 1971). This increase in numbers and shift in habitat use suggest that rails are now more exposed to Grey Herons than in the past and could explain why the reported predation has not been observed before.

The Grey Heron is the first recorded natural predator of the Aldabra White-throated Rail. As the last remaining flightless bird in the Indian Ocean, the conservation status of these rails could necessitate intervention if the population becomes threatened through increased Grey Heron predatory behavior.

ACKNOWLEDGMENTS

I am grateful to Adrian Skerret and two anonymous reviewers for comments that improved this manuscript. Seychelles Island Foundation provided logistical and financial support during the study.

LITERATURE CITED

Feare, C. J. and J. Watson. 1984. Occurrence of migrant birds in the Seychelles. Pages 559–574 *in* Biogeography and ecology of the Seychelles Islands (D. R. Stoddart, Editor). W. Junk Publishers, The Hague, Netherlands.

Gwiazda, R. and A. Amirowicz. 2006. Selective foraging of Grey Heron (*Ardea cinerea*) in relation to density and composition of the littoral fish community in a submontane dam reservoir. Waterbirds 29:226–232.

Jakubas, D. and A. Mioduszewska. 2005. Diet composition and food consumption of the Grey Heron (*Ardea cinerea*) from breeding colonies in northern Poland. European Journal of Wildlife Research 51:191–198.

Marquiss, M. and A. F. Leitch. 1990. The diet of Grey Herons *Ardea cinerea* breeding at Loch Leven, Scotland, and the importance of their predation on ducklings. Ibis 132:535–549.

McCanch, N. 2003. Grey Heron choking on Little Grebe. British Birds 96:86.

Milstein, P. L., I. Prestt, and A. A. Bell. 1970. The breeding cycle of the Grey Heron. Ardea 58:171–257.

Ogilvie, M. 2003. Grebes of the world. Bruce Coleman Books, Uxbridge, United Kingdom.

Penny, M. J. and A. W. Diamond. 1971. The White-throated Rail, *Dryolimnas cuvieri* on Aldabra. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 260:529–548.

Wanless, R. M. 2002. The reintroduction of the Aldabra Rail *Dryolimnas cuvieri aldabranus* to Picard Island, Aldabra Atoll. Thesis. University of Cape Town, South Africa.

Wanless, R. M. 2003. Can the Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus*) fly? Atoll Research Bulletin 508:1–9.

Wanless, R. M., J. Cunningham, P. H. R. Hockey, J. Wanless, R. W. White, and R. Wisemen. 2002. The success of a soft-release reintroduction of the flightless Aldabra Rail (*Dryolimnas cuvieri aldabranus*) on Aldabra Atoll, Seychelles. Biological Conservation 107:203–210.

Williams, A. J. and V. L. Ward. 2006. Sacred Ibis and Grey Heron predation of Cape Cormorant eggs and chicks; and a review of ciconiiform birds as seabird predators. Waterbirds 29:321–327.

The Wilson Journal of Ornithology 120(3):633–635, 2008

Purple Swamphens (*Porphyrio porphyrio*) Attempting to Prey upon Black Swan (*Cygnus atratus*) Eggs and Preying upon a Cygnet on an Urban Lake in Melbourne, Australia

Shandiya Balasubramaniam[1] and Patrick-Jean Guay[1,2]

ABSTRACT.—We report the predation of Black Swan (*Cygnus atratus*) eggs and cygnets by adult Purple Swamphens (*Porphyrio porphyrio*), a mostly-herbivorous species of rail, in Melbourne, Victoria, Australia. *Received 9 October 2007. Accepted 28 November 2007.*

The Purple Swamphen (*Porphyrio porphyrio*) is a large rail (males: 1,050 g; females: 850 g) whose range encompasses southern Africa, southern Asia, Papua New Guinea, Australia, and New Zealand (Marchant and Higgins 1993). Quantitative investigations into diets of Purple Swamphens in Australia and New Zealand demonstrated this species is almost completely herbivorous (Carroll 1966, Norman and Mumford 1985). Animal material constitutes only a minor part of the diet and is mainly represented by insects and arachnids (Carroll 1966, Norman and Mumford 1985). However, they have been reported to eat fish, lizards, and birds (Wheeler 1949, Oliver 1974). They have also been observed preying on nestlings and adults of different passerine species (McKenzie 1967, Egan 1992, Fitzsimons 2003), as well as eggs (Binns 1953, Fitzgerald 1966, Brown 1997) and ducklings from different waterfowl species including Chestnut Teal (*Anas castanea*) (van Tets 1965), Pacific Black Duck (*A. superciliosa*) (Nixon 1983, Bonser 1984), and domestic Muscovy Duck (*Cairina moschata*) (Lowe 1966). We present the first record of Purple Swamphens taking Black Swan (*Cygnus atratus*) eggs and cygnets.

OBSERVATIONS

Observations were conducted during an investigation of incubation behavior of Black Swans at Albert Park Lake (37° 50′ S, 144° 58′ E), an urban lake in the center of Melbourne, Victoria, Australia. We observed a Purple Swamphen's opportunistic attempt to prey on a Black Swan egg on 7 September 2007 at 1230 hrs EST during an agonistic encounter between an incubating male and another adult swan. The male swan was incubating the eggs at the nest when another adult swan came within close range (~1 m) of the nest. The incubating male swan stood up in a threat display, raising its wings. It then proceeded to swim beside the intruding swan while displaying its curled feathers. This escalated into a chase as the incubating male bit the other adult's tail and pursued it for a distance of ~100 m.

As soon as the incubating male swan had left, three swamphens gathered around the nest. One of them perched on the rim of the bowl and started pecking at one of the four eggs in the nest. This continued for 30 sec after which time the male swan returned to the nest and the swamphens scattered. The swan stood over the eggs and preened its feathers for 10 min, and then rearranged some of the nesting material within the nest. This particular incident was unsuccessful. However, we have observed Purple Swamphens feeding on swan eggs on three occasions and 38% of Black Swan nests in this population lost at least one egg to swamphens or other predators during the 2007 breeding season.

We witnessed the predation of a newly-hatched Black Swan cygnet by a Purple Swamphen on 4 September 2007. At 1500 hrs, a pair of breeding swans at their nest started hissing and flapping their wings; moments later we observed a Purple Swamphen running from the nest with a cygnet in its beak. Neither adult swan left the nest to pursue the swamphen, which ran under a nearby swamp

[1] Department of Zoology, University of Melbourne, Parkville, VIC 3010, Australia.

[2] Corresponding author; e-mail: p.guay@zoology.unimelb.edu.au

paperbark (*Melaleuca ericifolia*) shrub. The swamphen shook the cygnet vigorously by the neck and then proceeded to tear at the cygnet's bill while holding its body down with one foot. The swamphen may then have been alarmed by our presence because it stopped shaking the cygnet and stood still for ~1 min. During this time the cygnet was trying feebly to move away but the swamphen did not appear to take any notice of it. The swamphen then grabbed the cygnet by the neck and ran from us through the vegetation. It remained out of our sight for 3 min and then returned to the swamp paperbark shrub. It started picking at the dead cygnet's neck and breast area. After 5 min the swamphen again ran away, this time leaving the carcass behind. Upon examining the cygnet carcass, we noted that it had been decapitated. A cursory search of the nearby area did not reveal the location of the head. A few moments later, after we had moved away, we noticed the swamphen running back and forth carrying small pieces of cygnet between the carcass and a grass tussock. This continued for ~15 min, after which we lost sight of the swamphen. We presumed, but did not confirm, the tussock was a Purple Swamphen nest.

DISCUSSION

These observations constitute the first report of predation by Purple Swamphens on Black Swan eggs and cygnets. This cygnet predation event is similar to the descriptions of swamphen predation on Pacific Black Duck ducklings by Nixon (1983) and Bonser (1984). Gizzard content analyses suggest that Purple Swamphens are herbivorous (Carroll 1966, Norman and Mumford 1985), but gizzard analyses tend to underestimate the animal component (Swanson and Bartonek 1970, Briggs et al. 1985) due to the relatively rapid degradation of soft animal tissues in comparison to fibrous plant material and seeds (e.g., van Koersveld 1950). Egg yolk is unlikely to be detected in gizzard contents (Fitzgerald 1966). The methodology used by Carroll (1966) and Norman and Mumford (1985) may have underestimated the animal content in the diet of Purple Swamphens, but animal material is unlikely to represent a large part of the adult diet as it constituted less than 1% of the total food content in the gizzard analyses. Consumption of the prey was not observed (e.g., van Tets 1965) in most cases of predation on vertebrates by adult swamphens. Purple Swamphens are known to feed their chicks (Craig 1980) and adults have been observed feeding young pieces of flesh from frogs (Brown and Brown 1977) and European Starlings (*Sturnus vulgaris*) (Egan 1992). We did not observe the swamphen feeding chicks, but its behavior suggests that it was bringing food to another individual. Juvenile Purple Swamphens, similar to juvenile waterfowl (e.g., Sugden 1973), may be more carnivorous than adults due to higher protein requirements to meet the demands of growth and development. While adult Purple Swamphens are largely herbivorous, it appears they can opportunistically take advantage of new animal food sources as they become available to feed their young. Underestimation of the proportion of animal material in swamphen diets is likely due to a lack of juvenile samples and poor representation of animal material in gizzard contents.

ACKNOWLEDGMENTS

This study was supported by an ARC Discovery Grant DP0558607 awarded to R. A. Mulder and M. A. Elgar, and the David Hay Scholarship to Patrick-Jean Guay.

LITERATURE CITED

Binns, G. 1953. Birds of Terang, south-western Victoria. Emu 53:211–221.

Bonser, C. M. 1984. Purple Swamphen vs duck. Bird Observer 630:70.

Briggs, S. V., M. T. Maher, and R. P. Plamer. 1985. Bias in food habits of Australian waterfowl. Australian Wildlife Research 12:507–514.

Brown, M. 1997. Birds of the wetlands: Purple Swamphen. Bird Observer 774:9–10.

Brown, R. J. and M. N. Brown. 1977. Observations on swamphens breeding near Manjimup, W.A. Corella 1:82–83.

Carroll, A. I. K. 1966. Food habits of the Pukeko (*Porphyrio melanotus* Temminck). Notornis 13: 133–144.

Craig, J. L. 1980. Pair and group breeding behaviour of a communal gallinule, the Pukeko, *Porphyriop. melanotus*. Animal Behaviour 28:593–603.

Egan, K. 1992. Purple Swamphen's predation on European Starling. Australian Birds 26:84.

Fitzgerald, M. F. 1966. Letter. Notornis 13:222.

Fitzsimons, J. A. 2003. Purple Swamphen *Porphyrio porphyrio* killing a Noisy Miner *Manorina melanocephala* nestling. Corella 27:90.

Lowe, V. T. 1966. Notes on the Musk Duck. Emu 65: 279–290.

Marchant, S. and P. J. Higgins. 1993. Handbook of Australian, New Zealand and Antarctic birds. Volume 2. Raptors to Lapwings. Oxford University Press, Melbourne, Australia.

McKenzie, H. R. 1967. Foods of the Pukeko. Notornis 14:41–42.

Nixon, C. 1983. Ducked, by a Purple Swamphen! Bird Observer 623:114.

Norman, F. I. and L. Mumford. 1985. Studies on the Purple Swamphen, *Porphyrio porphyrio*, in Victoria. Australian Wildlife Research 12:263–278.

Oliver, W. R. B. 1974. New Zealand birds. Reed, Wellington, New Zealand.

Sugden, L. G. 1973. Feeding ecology of Pintail, Gadwall, American Wigeon and Lesser Scaup ducklings in Southern Alberta. Canadian Wildlife Service Report Series 24:1–43.

Swanson, G. A. and J. C. Bartonek. 1970. Bias associated with food analysis in gizzards of Blue-winged Teal. Journal of Wildlife Management 34: 739–746.

van Koersveld, E. 1950. Difficulties in stomach analysis. Proceedings of the International Ornithological Congress 10:592–594.

van Tets, G. F. 1965. Eastern Swamphen takes a downy from a pair of Chestnut Teal. Emu 64:100.

Wheeler, R. 1949. Nature notes. Bird Observer's Club Monthly Notes 212(July 1949):1.

The Wilson Journal of Ornithology 120(3):635–636, 2008

Northern Fulmar Predation of Common Murre

Stephan Lorenz[1,2] and Sampath Seneveratne[1]

ABSTRACT.—We observed a Northern Fulmar (*Fulmarus glacialis*) prey upon a live Common Murre (*Uria aalge*) off Cape Spear, Newfoundland, Canada on 4 November 2007. Active predation of Northern Fulmars on other seabirds has not previously been reported. *Received 19 November 2007. Accepted 16 January 2008.*

Northern Fulmars (*Fulmarus glacialis*) are widespread throughout the northern Atlantic and Pacific oceans and populations have increased in Atlantic Canada (Stenhouse and Montevecchi 1999). The diet of Northern Fulmars includes a wide range of fish, squid, copepods, amphipods and, to a lesser extent, polychaetes, pteropods, and cnidarians (Camphuysen and van Franeker 1996, Hatch and Nettleship 1998, Phillips et al. 1999). In addition, Northern Fulmars also feed on offal and carrion, mainly fish refuse and remains of marine mammals (Fisher 1952, Hobson and Welch 1992, Camphuysen and Garthe 1997). They forage by dipping, surface seizing, surface plunging (Hatch and Nettleship 1998, Brooke 2004), and pursuit diving (Hobson and Welch 1992, Garthe and Furness 2001, Brooke 2004). Fulmars have been observed scavenging carcasses of birds, including cannibalism (Fisher 1952). Fisher (1952) also cites indirect evidence of fulmars eating wounded birds, direct observations of attacking gulls (Laridae), and one captive fulmar killing, but not consuming a European Greenfinch (*Carduelis chloris*).

OBSERVATIONS

We report a previously undocumented foraging behavior and prey item of the Northern Fulmar. On 4 November 2007 while watching seabird congregations off Cape Spear, Newfoundland (47° 31′ 25″ N, 52° 37′ 13″ W) we observed a fulmar kill and feed on a Common Murre (*Uria aalge*). At 0930 hrs (NST) after ~2 hrs of continued observation of seabirds passing close to land, consisting of large numbers of Dovekies (*Alle alle*) and smaller numbers of Common and Thick-billed (*U. lomvia*) murres, Razorbills (*Alca torda*), and Black-legged Kittiwakes (*Rissa tridactyla*), we observed a light phase fulmar actively pursuing a winter plumage Common Murre. Both birds were ~50 m offshore and were observed through binoculars and a spotting scope. Initially the fulmar was seen biting the murre's neck while both birds were sitting on the wa-

[1] Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

[2] Corresponding author; e-mail: slorenz@mail.com

ter. As the struggle continued the fulmar persistently clasped the murre by the bill and neck, apparently in an attempt to drown it. The murre freed itself several times only to dive for a few seconds and being attacked on resurfacing. The entire struggle lasted 15 min until the murre had succumbed, floating on the surface. The fulmar proceeded to feed on the dead bird, plucking at the vent area. Great Black-backed Gulls (*Larus marinus*) harassed the feeding fulmar, which actively and successfully defended its prey using aggressive postures. We continued to observe the fulmar for another 30 min and it was still feeding on and defending the murre carcass when we left.

DISCUSSION

We found no previous reports of Northern Fulmar actively preying on seabirds or procellariid species preying upon alcids. Only the Southern (*Macronectes giganteus*) and Northern Giant (*M. halli*) petrels within the family Procellariidae regularly prey on seabirds, mainly penguins (Spheniscidae) at breeding colonies (Brooke 2004). Fisher (1952) reports Northern Fulmars scavenging Rhinoceros Auklet (*Cerorhinca monocerata*) and Puffin (*Fratercula* spp.). Documented predators of adult Common and Thick-billed murres, and the related Razorbill include a wide range of large raptors and mammals, especially foxes (*Alopex lagopus* and *Vulpes vulpes*) and, at times, polar bears (*Ursus maritimus*) (Gaston and Hipfner 2000, Ainley et al. 2002, Hipfner and Chapdelaine 2002). Common Murres appear to be high-risk prey items for fulmars (body mass 600–700 g) due to their large body size (>800 g) and powerful beak. We conclude that fulmar predation of sympatric seabirds is a rare event, in this case possibly triggered by unfavorable weather leading to decreased feeding or a purely opportunistic event due to a sick or exhausted bird. We were unable to judge the condition of the murre, but believe that the bird was relatively healthy due to the vigorous defense and prolonged struggle. Common Murres are one of the largest Atlantic alcids; thus, Northern Fulmars could potentially prey on other seabirds, especially many of the smaller alcids.

ACKNOWLEDGMENTS

We thank C. E. Braun and two anonymous reviewers who provided useful comments on this manuscript.

LITERATURE CITED

Ainley, D. G., D. N. Nettleship, H. R. Carter, and A. E. Storey. 2002. Common Murre (*Uria aalge*). The birds of North America. Number 666.

Brooke, M. 2004. Albatrosses and petrels across the world. Oxford University Press, New York, USA.

Camphuysen, C. J. and S. Garthe. 1997. Distribution and scavenging habits of Northern Fulmars in the North Sea. Journal of Marine Science 54:654–683.

Camphuysen, C. J. and J. A. van Franeker. 1996. Jellyfish and fishery waste as food sources of Northern Fulmars *Fulmarus glacialis* feeding around St. Kilda. Sula 10:143–150.

Fisher, J. 1952. The fulmar. Collins, London, England.

Garthe, S. and R. W. Furness. 2001. Frequent shallow diving by a Northern Fulmar at Shetland. Waterbirds 24:287–289.

Gaston, A. J. and J. M. Hipfner. 2000. Thick-billed Murre (*Uria lomvia*). The birds of North America. Number 497.

Hatch, S. A. and D. N. Nettleship. 1998. Northern Fulmar (*Fulmarus glacialis*). The birds of North America. Number 361.

Hipfner, J. M. and G. Chapdelaine. 2002. Razorbill (*Alca torda*). The birds of North America. Number 635.

Hobson, K. A. and H. E. Welch. 1992. Observations of foraging Northern Fulmars (*Fulmarus glacialis*) in the Canadian high arctic. Arctic 45:150–153.

Phillips, R. A., M. K. Petersen, K. Lilliendahl, K. Solmundsson, K. C. Hamer, C. J. Camphuysen, and B. Zonfrillo. 1999. Diet of the Northern Fulmar *Fulmarus glacialis*: reliance on commercial fisheries? Marine Biology 135:159–170.

Stenhouse, I. J. and W. A. Montevecchi. 1999. Increasing and expanding populations of breeding Northern Fulmars in Atlantic Canada. Waterbirds 22:382–391.

The Wilson Journal of Ornithology 120(3):637–640, 2008

Diet of Nestling Black-crowned Night-herons in a Mixed Species Colony: Implications for Tern Conservation

C. Scott Hall[1,3,4] and Stephen W. Kress[1,2]

ABSTRACT.—Boluses were collected from Black-crowned Night-heron (*Nycticorax nycticorax*) nestlings in 1992 to examine the impact of night-heron predation on a restored tern colony. Boluses (n = 101) were collected from 18 nests. Fish remains occurred in 89% of nests, sand shrimp (*Crangon septemspinosa*) in 50%, birds in 28%, and amphibians in 16% of nests sampled; mammalian, eel, squid, and marine invertebrate remains were also noted. Regurgitated bird remains were found in five nests and included four species, Common Terns (*Sterna hirundo*), Common Eiders (*Somateria mollissima*), Gulls (*Larus* sp.), and the legs of an unknown wading bird. Nestling night-herons from three nests were fed tern chicks, but 92% of tern chicks known to have been eaten were fed to nestling Black-crowned Night-herons in one nest. No tern chicks fledged in 1992 and night-herons were observed in the tern colony on multiple occasions. This study suggests that individual night-herons will specialize on waterbird prey. The subsequent removal of a specialist night-heron predator resulted in improved tern productivity. *Received 16 February 2007. Accepted 16 October 2007.*

Black-crowned Night-herons (*Nycticorax nycticorax*) are a generalist predator with a varied diet, which includes fish, mollusks, crustaceans, mammals, amphibians, reptiles, invertebrates, vegetation, and bird eggs and chicks (Marshall 1942, Palmer 1962, Collins 1970, Wolford and Boag 1971, Szlivka 1985, Yen 1991, Davis 1993). They are reported to feed by sight (Watmough 1978) and sound (Hunter and Morris 1976), and will take advantage of temporary abundances of food (Davis 1993). Food preference is reported to vary between colonies and years (Collins 1970). Night-heron predation in colonial waterbird colonies has been widely noted (Beckett 1964, Collins 1970, Hunter and Morris 1976, Nisbet and Welton 1984) and negative impacts have been documented on nesting colonial seabirds (Hunter and Morris 1976, Shealer and Kress 1991).

Stratton Island is a diverse waterbird colony in Maine that provides habitat for both a restored nesting colony of terns (Arctic [*Sterna paradisaea*], Common [*S. hirundo*], Least [*S. antillarum*], and Roseate [*S. dougallii*]) (Kress [1983] provides a discussion of tern restoration techniques) and nesting wading birds including Black-crowned Night-herons. Nocturnal losses of tern eggs and chicks were first observed in 1989, 3 years after tern restoration was initiated. Tern reproductive success was poor in 1989 (0.07 chicks/pair; Shealer 1989) and 1991 (0.0 chicks/pair; Hedges and Whitaker 1991), and good in 1990 (1.5 chicks/pair; Skinner 1990) when productivity monitoring only occurred in an area where startle lights were used to deter night-heron predation. Overall, recruitment to the tern colony slowed during this period and birds were abandoning the colony at night and between seasons. Observations of terns mobbing adult and juvenile night-herons in or adjacent to the tern colony were recorded from 1989 to 1992, but night-herons were only observed taking tern chicks and eggs in 1992 (Benz and D'Angelo 1992).

The objectives of our study were to: (1) quantify Black-crowned Night-heron nestling diet, (2) identify the number of night-heron pairs that were feeding terns to their young, and (3) examine the impact of night-heron predation on a tern colony.

METHODS

Study Area.—The study was conducted in 1992 on Stratton Island (43° 31′ N, 70° 19′

[1] National Audubon Society, Seabird Restoration Program, 12 Audubon Road, Bremen, ME 04551, USA.

[2] Current address: National Audubon Society, Seabird Restoration Program, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.

[3] Current address: National Audubon Society, Seabird Restoration Program, 118 High Street, Suite 2, #26, Belfast, ME 04915, USA.

[4] Corresponding author; e-mail: shall@audubon.org

TABLE 1. Black-crowned Night-heron nestling diet, Stratton Island, Maine, 1992. Frequency equals the number of nests containing the designated prey type and not the total number of individuals recovered for each prey type.

Prey item	Nests (n = 18) Frequency of nests (%)
Bird	5 (27.7)
Sterna sp.	3 (16.7)
Larus sp.	3 (16.7)
Somateria mollissima	3 (16.7)
Unk - ardeid	2 (11.1)
Unk - bird	1 (5.6)
Fish	16 (88.9)
Unknown fish	16 (88.9)
Alosa pseudoharangus	1 (5.6)
Catostomus sp.	1 (5.6)
Fundulus majalis	1 (5.6)
Unk - Catfish	1 (5.6)
Sand Shrimp (*Crangon septemspinosa*)	9 (50.0)
Amphibian	3 (16.7)
Rana clamitans	2 (11.1)
Rana sp.	1 (5.6)
Eel	1 (5.6)
Mammal	1 (5.6)
Tamais striatus	1 (5.6)
Invertebrate	2 (11.1)
Squid	1 (5.6)

W), 3 km east of Prout's Neck, York County, Maine. The National Audubon Society's Seabird Restoration Program monitors and manages this mixed species, 12.2-ha inshore island. Stratton Island has been Maine's most diverse waterbird colony with 21 nesting species; in 1992, the wading bird colony included ~250 pairs of Snowy Egret (*Egretta thula*), Little Blue Heron (*E. caerulea*), Tri-colored Heron (*E. tricolor*), Cattle Egret (*Bubulcus ibis*), Glossy Ibis (*Plegadis falcinellus*), and Black-crowned Night-heron.

Bolus Collection and Processing.—Night-heron nests were flagged during the annual wading bird census for subsequent visits. We collected spontaneous regurgitations from captured nestlings and obtained additional boluses by gently massaging the neck of captured nestlings. Samples were labeled, placed in plastic bags and preserved in a 70% ethanol solution for future processing. Samples were not collected from every nest on each visit to reduce disturbance.

The colony contained 53 night-heron pairs and 18 of the nests were included in the study. Nest inclusion was dependent on hatching fate, chick survival, and our ability to sample nestlings (nests at the top or on outer branches of a nesting tree could not be sampled). Nests were visited 5–14 times between 11 June and 7 August while tern chicks were present on the island. One to 33 samples were collected from each nest (mode = 4 samples/nest).

Samples were identified in January 1993 to the most precise taxa possible by initially sorting bolus contents by size and taxa. The contents were screened by passing water over the boluses and through a hardware cloth sieve. Voucher specimens were preserved in glass jars with 70% ethanol. All bird remains and fish scales (mounted on slides) were washed (feathers were dried) before examination under a stereo dissecting scope. Unidentified fish samples were submitted to the Maine Department of Marine Resources for identification.

Tern Monitoring.—An annual nest census was conducted by walking through the tern colony and marking all nests following the procedures of Kress and Hall (2004). The count was timed to coincide with the maximum number of nests prior to hatch. Two hundred and twenty-one pairs of Common Terns, seven pairs of Roseate Terns, and five pairs of Arctic Terns nested in 1992. Productivity (fledglings produced/pair) was measured from a sample of nests (n = 25) in five enclosures, which were enclosed to permit recapture of chicks. Enclosures measured 7.62 × 3.66 m and were constructed from chicken wire wrapped with landscape fabric. Enclosure locations were random and constructed in tern nesting habitat prior to clutch initiation. All chicks were banded within 1 day of hatching with a USGS band and followed through fledging.

RESULTS

One hundred and one boluses were collected from Black-crowned Night-heron nestlings; 58% contained bird remains, 33% fish, and 16% sand shrimp. However, sixty-two boluses were collected from just three nests. Additional prey items (small proportions) included eel, squid, amphibians, mammals, and insects. Fish were found at 89% of the sampled nests, sand shrimp at 50%, and bird remains at 28% (n = 5). Fifty percent (39 total sam-

ples) of the bird remains were tern chicks (most were *S. hirundo*), 24% (19 total samples) were Common Eider ducklings, and 22% (18 total samples) were gull chicks (either *L. argentatus* or *L. marinus*). Most bird remains (97%) were found at three nests and 92% of the tern chick remains were in one nest including 21 of 22 recovered tern bands from a total available sample of 66 banded Common Tern chicks. Remains of gull chicks and eider ducklings were found in three nests, although 70% of gull chicks were found at one nest (different than the nest with tern chicks) and 53% of eider ducklings were found in another nest.

No tern chicks fledged from enclosures in 1992. Sixty-five eggs were laid in 25 enclosure nests, 26 disappeared (6 were pipping), 12 were abandoned, 2 were depredated, and 25 hatched. All hatched chicks disappeared before they reached 8 days of age; 18 disappeared by the age of 3 days. We assumed all chicks that disappeared were predated as no remains were found within or outside enclosures and night-herons were observed feeding in the colony.

DISCUSSION

Black crowned Night-heron nestlings on Stratton Island were fed a diverse diet consisting of marine, tidal/estuary, freshwater, and upland-derived vertebrate and invertebrate prey. Fish (4+ species), shrimp, and birds (4+ species) were the dominant prey by frequency in boluses and at nests. Unlike other studies (Szlivka 1985, Yen 1991), amphibians occurred in less than 5% of boluses, suggesting that night-herons nesting on Stratton Island forage primarily in marine or estuarine habitats, rather than freshwater habitat. Most food habit studies or summaries of Black-crowned Night-heron diets have reported that fish were the principal food (Collins 1970, Hoffman 1978, Szlivka 1985, Yen 1991, Davis 1993, Riehl 2006) but, in this study, while fish occurred in 89% of nests, shrimp and bird remains occurred in greater numbers and frequency in boluses. Bird remains have been reported in many other food studies of night-herons (Collins 1970, Wolford and Boag 1971, Hunter and Morris 1976, Yen 1991). The presence of wading bird remains in night-heron boluses is also consistent with other studies (Beckett 1964, Wolford and Boag 1971, Riehl 2006).

Although bird remains were prevalent, nestlings at only five of 18 nests were provisioned with birds and, of these, 97% of bird remains were at three nests. Parents at only one of these three nests provisioned their young exclusively with birds and this pair concentrated on gulls, but also delivered eider ducklings and tern chicks. Tern chicks were observed at all three nests with bird remains, but 92% of tern remains (36 of 39 total tern remains) were concentrated at one nest. However, 49% of the diet at this nest was comprised of sand shrimp (and 1 green frog [*Rana* sp.]); 51% were bird remains (11% gulls, 13% eiders, 76% terns) suggesting that each adult in this pair had specific food or foraging habitat preferences. Thus, night-heron predation in this tern colony appeared to be a specialized feeding behavior with just one adult consistently using this food resource.

Despite the low frequency of this specialized feeding behavior by night-herons, the consequences for nesting terns on Stratton Island were pronounced. No tern chicks fledged from study nests in 1992. Direct predation (inferred from predated eggs, missing young chicks, and from direct observation of predation with night vision binoculars) by night-herons was the principal cause of mortality in 1992. Several other studies have noted significant impacts of night-heron predation on tern reproductive success (Collins 1970, Hunter and Morris 1976, Nisbet and Welton 1984, Shealer and Kress 1991).

A single adult Black-crowned Night-heron was shot on 5 July 1994 while feeding on tern chicks. No additional predation by night-herons was noted in the tern colony in 1994. Night-heron predation was not observed again on Stratton Island until 2002. In response to the removal of one night-heron, tern productivity increased to 1.9 chicks/nesting pair in 1994. The average tern productivity during years of night-heron predation (1989–1993, 2002) was 0.42 chicks/pair and, with no observed night-heron predation, it was 1.6 chicks/pair from 1994 to 2001. This suggests that night-heron predation was a major factor in affecting tern nesting success on Stratton Island.

Night-heron predation can have significant

impacts on nesting waterbirds and the exploitation of tern chicks is likely a specialized feeding behavior. The subsequent removal of an individual night-heron and corresponding positive breeding response by terns suggests that removal of specialist night-heron predators can reduce impacts to nesting terns.

ACKNOWLEDGMENTS

Funding was provided by grants and donations to the National Audubon Society Seabird Restoration Program and by the Prout's Neck Chapter of the National Audubon Society. We thank Stephanie Schmidt of the Manomet Center for Conservation Sciences for comments on the manuscript. We are grateful to Charlie and Sally Lee for their generous hospitality. We thank the field teams for vigilantly collecting regurgitated samples. We are especially indebted to Eric Kershner for processing samples and preparing a report of the bolus collection effort. We also thank Jean Chenoweth from the Maine Department of Marine Resources Laboratory in West Boothbay for assistance with fish identification and Charles Dardia of the Cornell Vertebrate Collections for assistance and laboratory space.

LITERATURE CITED

Beckett, T. A. 1964. Black-crowned Night-heron feeding behavior. Chat 29:93–94.

Benz, S. and P. D'Angelo. 1992. Stratton and Bluff islands, The National Audubon Society's Phineas W. Sprague Memorial Sanctuary, Saco Bay, Maine. 1992 Season Report. National Audubon Society Seabird Restoration Program, Ithaca, New York, USA.

Collins, C. T. 1970. The Black-crowned Night-heron as a predator of tern chicks. Auk 87:584–586.

Davis, W. E. 1993. Black-crowned Night-heron. The birds of North America. Number 74.

Hedges, S. and H. Whitaker. 1991. Stratton and Bluff islands, The National Audubon Society's Phineas W. Sprague Memorial Sanctuary, Saco Bay, Maine. 1991 Season Report. National Audubon Society Seabird Restoration Program, Ithaca, New York, USA.

Hoffman, R. D. 1978. The diets of herons and egrets in southwestern Lake Erie. Pages 365–369 *in* Wading birds (A. Sprunt IV, J. C. Ogden, and S. Winkler, Editors). Research Report Number 7. National Audubon Society, New York, USA.

Hunter, R. A. and R. Morris. 1976. Nocturnal predation by a Black-crowned Night-heron at a Common Tern colony. Auk 93:629–633.

Kress, S. W. 1983. The use of decoys, sound recordings, and gull control for re-establishing a tern colony in Maine. Colonial Waterbirds 6:185–196.

Kress, S. W. and C. S. Hall. 2004. Tern management handbook: coastal northeastern United States and Atlantic Canada. USDI, Fish and Wildlife Service, Hadley, Massachusetts, USA.

Marshall, N. 1942. Night desertion by nesting Common Terns. Wilson Bulletin 54:25–31.

Nisbet, I. C. T. and M. J. Welton. 1984. Seasonal variations in breeding success of Common Terns: consequences of predation. Condor 86:53–60.

Palmer, R. S. 1962. Handbook of North American birds. Volume 1. Loons through flamingos. Yale University Press, New Haven, Connecticut, USA.

Riehl, C. 2006. Widespread cannibalism by fledglings in a nesting colony of Black-crowned Night-herons. Wilson Journal of Ornithology 118:101–104.

Shealer, D. A. 1989. Stratton and Bluff islands, The National Audubon Society's Phineas W. Sprague Memorial Sanctuary, Saco Bay, Maine. 1989 Season Report. National Audubon Society Seabird Restoration Program, Ithaca, New York, USA.

Shealer, D. A. and S. W. Kress. 1991. Nocturnal abandonment response to Black-crowned Night-heron disturbance in a Common Tern colony. Colonial Waterbirds 14:51–56.

Skinner, J. M. 1990. Stratton and Bluff islands, The National Audubon Society's Phineas W. Sprague Memorial Sanctuary, Saco Bay, Maine. 1990 Season Report. National Audubon Society Seabird Restoration Program, Ithaca, New York, USA.

Szlivka, L. 1985. Data on the food of the Purple (*Ardea purpurea*), Night (*Nycticorax nycticorax*) and Squacco (*Ardeola ralloides*) herons on Lake Ludas. Larus 36–37:175–182.

Watmough, B. R. 1978. Observations on nocturnal feeding by night-herons (*Nycticorax nycticorax*). Ibis 120:356–358.

Wolford, J. W. and D. A. Boag. 1971. Food habits of Black-crowned Night-herons in southern Alberta. Auk 88:435–437.

Yen, Chung-Wei. 1991. Food of nestling egrets and night herons in the western lowlands of central Taiwan. Journal of the Taiwan Museum. 44:309–320.

The Wilson Journal of Ornithology 120(3):641–645, 2008

Diet of the Long-eared Owl in the Northern and Central Negev Desert, Israel

Zohar Leader,[1] Yoram Yom-Tov,[2,3] and Uzi Motro[1]

ABSTRACT.—This is the first report of the diet composition of Long-eared Owl (*Asio otus*) in the northern and central Negev desert, Israel. The diet consisted of 71.3% small mammals, 26.5% birds, 2.0% invertebrates, and 0.1% reptiles. There were no significant differences among the seven localities studied or among seasons in percent rodents or invertebrates in the diet. However, the proportion of psammophilious rodents within the diet was larger in settlements where the soil was sand or sandy-loess and smaller where the soil was loess or rocky. Percent birds in the diet did not differ among localities, but differed among seasons. Migratory birds formed a significantly larger part of the total birds consumed during migration than during the non-migratory months. *Received 15 August 2007. Accepted 24 December 2007.*

The Long-eared Owl (*Asio otus*) is a Holarctic, nocturnal bird of prey whose diet has been extensively studied in North America and Europe. The literature on its diet indicates that it feeds mainly on rodents, especially voles, and other small mammals, complemented by other animals, including birds and invertebrates (Cramp and Simmons 1985). It forages in the open, but also hunts near and below trees (Cramp and Simmons 1985) where it feeds on birds that roost in trees. In Israel there are resident, migratory, and wintering populations of Long-eared Owls (Paz 1987, Shirihai 1996). The species inhabits most low-lying areas in Israel, chiefly in the Mediterranean region, but also in agricultural settlements in the desert during the last three decades. This species prefers semi-open areas in Israel such as agricultural settlements, plantations, and patches or lines of trees (Shirihai 1996). The diet of the Long-eared Owl has not been studied in Israel. We collected data on the diet of the Long-eared Owl and report on the composition of the diet in the northern and central Negev desert, Israel.

[1] Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, Jerusalem 91904, Israel.

[2] Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel.

[3] Corresponding author; e-mail: yomtov@post.tau.ac.il

METHODS

We studied Long-eared Owls in the northern and central Negev, Israel, a relatively arid region where rain occurs only during winter (Nov–Apr). Annual precipitation ranges between 300 mm in the north to 100 mm in the south and varies greatly from year to year. Mean monthly temperature ranges between 26° C in July and 11° C in January (Jaffe 1986).

We located communal winter roosts of Long-eared Owls and nesting sites during the breeding season in or near agricultural settlements; these were visited once or twice every month between May 2002 and December 2003. Long-eared Owls roost in dense vegetation which, in our study area, occurs only in settlements. All pellets were collected during each visit and the area was cleaned of pellets and remains of prey; each collection was composed of "fresh" pellets accumulated since the last visit. Each pellet was placed in a separate bag and its date and locality were recorded. All pellets were allocated to one of four seasons: winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and autumn (Sep–Nov). Pellets were identified by their gray or light-black color and relatively (in comparison with those of the sympatric Barn Owl [*Tyto alba*]) narrower width, and with duller color. Pellets where species identification was not clear were not used. Each pellet was either separated to its components in the laboratory using tweezers or soaked in water until the remains, and cranial and post-cranial elements

could be separated. Species identification was by comparison with identified specimens in the collection of the Zoological Museum of Tel Aviv University and the collection of The Hebrew University of Jerusalem.

We treated each single pellet as a unit containing the remains of the complete portion of food eaten. Bones of one prey item under field conditions usually appear in one pellet and only rarely are they discarded in two or more pellets (Raczyński and Ruprecht 1974). However, there is the possibility that owls will cache large prey items and return to them later. In these cases, over estimation of the large prey items would occur using our pellet analysis. Our data suggests that over estimation could have occurred for only one prey species (*Rattus rattus*) in one locality (Nirim).

The main identifiable elements were crania, mandibles, and femura for mammals, skulls and humeri for birds, mandibles for reptiles, and exoskeleton pieces for invertebrates. The minimum number of individuals (MNI) was calculated from the most common element for every species. All remains in the pellets were identified to the lowest possible taxon. Differences between species were often small and most remains were identified to genus. A small proportion (2–11%) of post cranial remains could not be identified to genus. These remains belonged to either *Meriones* or *Gerbillus* (Gerbilidae) and we divided them between the two genera by their relative amount actually found in the identifiable remains. Identified bird species were categorized by their status in Israel (residents or migrants). However, some bird genera and even species have both resident and migratory populations in Israel. The remains in these cases were categorized to the status of the most common species in the genus in the study area.

The seven settlements from which we collected pellets were (number of pellets collected in parentheses): Sde Boqer 30° 52′ N, 34° 48′ E (280 pellets), Revivim 31° 03′ N, 34° 44′ E (380), Gevulot 31° 12′ N, 34° 28′ E (340), Tse'elim 31° 12′ N, 34° 32′ E (97), Tzohar settlements (a group of 6 settlements within 1–2 km) 31° 14′ N, 34° 25′ E (480), Omer 31° 17′ N, 34° 50′ E (157), and Nirim 31° 19′ N, 34° 22′ E (1,300).

All but one (Omer) of the sites were agricultural settlements, and all had ornamental trees, bushes, and grass lawns. The surrounding fields contained agricultural crops (potatoes, peanuts, carrots, etc.) as well as plantations (olives, avocado) and had lines of or scattered ornamental trees (various genera of palms, *Tamarisk* ssp., *Acacia* ssp.). The natural small mammalian fauna consists of several species of rodents and shrews with a strong psammophilous element where loess soil was mixed with sand. Commensal rodents (mice and rats) were also present.

We used two-way ANOVA tests for each of the three food categories (rodents, invertebrates, and birds) to test if there were differences in diet composition among localities and seasons. We used the Shannon-Wiener Index to calculate a value for diet diversity for each locality and two-way ANOVAs to test differences in diet diversity among localities and seasons.

RESULTS

We collected 3,034 pellets of Long-eared Owls, comprising 4,668 prey items with a composition of 71.3% small mammals, 26.5% birds, 2.0% invertebrates, and 0.1% reptiles (Table 1). There were no significant differences among localities or among seasons in percent rodents (P-values were 0.331 and 0.076, respectively) nor in percent invertebrates (P = 0.513 and P = 0.473, respectively) in the diet. Percent birds in the diet did not differ among localities (P = 0.144), but differed among seasons (P = 0.037). There were no significant differences in diet diversity (Shannon-Wiener Index) among localities (P = 0.290) or among seasons (P = 0.803).

There were no differences in percent rodents (as a group) in the diet among localities, but rodent genera composition differed among localities: percent *Gerbillus* among rodents changed from 63–70% in Gevulot, Revivim, and Tse'elim to 43% in Tzohar, and 16% in Sde Boqer, and only 1–2% in Nirim and Omer, while the proportion of *Meriones* was highest (42–46%) in Nirim and Omer, 17–20% in Revivim, Tse'elim, Gevulot, and Tzohar and 10% in Sde Boqer. *Jaculus* composed 9, 6, and 1% in Revivim, Sde Boqer, and Gevulot, respectively. Commensal species comprised 67% (*Mus* only) of the rodents in Sde Boqer, 56% (30% *Mus* and 26% *Rattus*) in Nirim (with a possible risk of over estimation

TABLE 1. Genera and species identified in Long-eared Owl pellets. (n = number of individuals in each taxonomic class; % = percent of these individuals among the total number of individuals in the pellets).

Mammalia (n = 3,327; 71.3%)	
Rodentia	
Acomys spp.	
Gerbillus spp.	
Jaculus jaculus	
Meriones spp.	
Microtus guentheri	
Mus musculus	
Rattus rattus	
Spalax ehrenbergi	
Soricomorpha	
Crocidura spp.	
Chiroptera	
Otonycteri hemprichii	
Pipistrellus spp.	
Aves (n = 1,236; 26.5%)	
Passeriformes	
Alaudidae sp.	
Carduelis carduelis	
C. chloris	
Cercomela melanura	
Emberiza spp.	
Fringilla coelebs	
Hippolais spp.	
Hirundo spp.	
Lanius spp.	
Motacilla spp.	
Nectarinia osea	
Oenanthe spp.	
Passer domesticus	
Coraciiformes	
Merops apiaster	
Galliformes	
Coturnix coturnix	
Reptilia (n = 3; 0.1%)	
Squamata	
Gekkonidae sp.	
Scincidae sp.	
Insecta (n = 93; 2.0%)	
Blattodea	
Blattidae sp.	
Coleoptera	
Scarabaeus spp.	
Curculionidae sp.	
Hymenoptera	
Dorylus fulvus	
Mantodea sp.	
Orthoptera	
Gryllidae sp.	
Gryllotalpa gryllotalpa	
Arachnida (n = 2; 0.0%)	
Solifugae sp.	
Unidentified (n = 7; 0.1%)	

of *Rattus* in the pellets), 52% (42% *Mus* and 10% *Rattus*) in Omer, and 37, 18, and 11% in Tzohar, Tse'elim, and Gevulot, respectively.

We found a total of 1,236 bird remains (Table 1) and identified 881 of them. These belonged to at least 23 species, and between 31 and 85% of which (depending upon location) were House Sparrows (*Passer domesticus*). Percent birds in the diet differed significantly among seasons. The number of remains of resident birds was 156, 92, 203, and 295 in autumn, winter, spring, and summer, respectively, while the respective numbers for migrants were 33, 11, 73, and 18. The number of resident bird remains was similar during the migratory (spring and autumn) and non-migratory (winter and summer) seasons (359 and 387, respectively), but the number of migrant remains, which consisted mainly of small passerines, was 3.7 times larger during the migratory seasons than during the non-migratory period (106 and 29, respectively). Thus, migratory birds comprised a significantly larger part (of the total birds consumed) during migration than during the non-migratory months (Fisher's exact test, $P = 2 \times 10^{-11}$).

DISCUSSION

The diet of the Long-eared Owl in North America, Europe, and Japan is composed mainly of voles (Glue and Hammond 1974; Marti 1974, 1976; Nilsson 1981; Village 1981; Marks 1984; Bosakowski and Smith 1991; Tome 1994; Capizzi et al. 1998; Alivizatos and Goutner 1999; Navarro et al. 2003; Chiba et al. 2005). The one species of vole in the Mediterranean region in Israel (*Microtus guentheri*) is not found in the desert and occurs only in the northern part of our study area. We found only three voles in the diet of the Long-eared Owl (at Nirim, the most northern of our localities). The main species of prey in our study area were gerbils, jirds, mice, and rats. We believe the proportions of rodent species in the diet of the Long-eared Owl reflects the composition of the rodent communities where the pellets were collected. The soil in our study area is either sand or loess (wind deposited) or a mixture of different proportions of these two types. There are four species of psammophile *Gerbillus* (*G. pyramidum*, *G. allenbyi*, *G. gerbillus*, and *G. henleyi*) and one non-psammophile (*G. dasyurus*) that

occurs mainly in rocky habits. The diet of the Long-eared Owl in areas where the soil was sandy or had a large proportion of sand (Revivim, Gevulot, and Tse'elim) was mainly *Gerbillus* (63–70% of the rodents in the diet), while in loess-dominated areas (Nirim, Omer, Sde Boqer) it was below 17%. The proportion of *Gerbillus* constituted 43% of the rodents in Tzohar, where the soil is sandy-loess. *Gerbillus* was replaced by other rodents, mainly *Meriones*, where the soil was not sandy. Commensal rodents (house mouse [*Mus musculus*] and black rat [*Rattus rattus*]) comprised >50% of the diet in Sde Boqer, Nirim, and Omer. The high proportion of house mice in the diet in Sde Boqer is explained by a mice plague that occurred there in 2003, while the high proportion of commensal species in Omer is probably the result of this being an urban suburb of the city of Beer Sheva. Jerboas (*Jaculus jaculus*) occur on both types of soil, and occurred in a low proportion in Revivim (sand) and Sde Boqer (loess).

The numbers of resident bird remains were similar during the migratory (spring and autumn) and non-migratory (winter and summer) seasons (359 and 387, respectively). The number of remains of migrant birds was 3.7 times larger during the migratory season than during the non-migratory period (106 and 29, respectively).

The Long-eared Owl has been characterized as having a more specialized diet than other sympatric owls (Marti 1976, Andrews 1990). Other studies (Marks 1984, Bertolino et al. 2001) demonstrated that Long-eared Owls feed opportunistically. Our study indicates the diet of the Long-eared Owl in the northern and central Negev desert consists mainly of rodents (71.3%), but also of birds (26.5%). The proportion of psammophilious rodents within the diet was large in settlements where the soil was sand or sandy-loess, and small where the soil was loess or rocky, and the proportion of migratory birds was 3.7 times larger during migratory seasons than during non-migratory periods. These variations reflect the availability of the different prey types, and suggest a noticeable plasticity and an opportunistic feeding behavior of the Long-eared Owl.

ACKNOWLEDGMENTS

We are grateful to Yoav Motro, Miriam Belmaker, Noam Leader, Mali Tores, Eran Levin, Leonid Friedman, Asaf Tsoar, Boaz Shacham, Igor Gavrilov, and three reviewers for their help, advice, and comments.

LITERATURE CITED

Alivizatos, H. and V. Goutner. 1999. Winter diet of the Barn Owl (*Tyto alba*) and Long-eared Owl (*Asio otus*) in northeastern Greece: a comparison. Journal of Raptor Research 33:160–163.

Andrews, P. 1990. Owls, caves and fossils. Natural History Museum Publications, London, United Kingdom.

Bertolino, S., E. Ghiberti, and A. Perrone. 2001. Feeding ecology of the Long-eared Owl (*Asio otus*) in northern Italy: is it a dietary specialist? Canadian Journal of Zoology 79:2192–2198.

Bosakowski, T. and D. G. Smith. 1991. Comparative diets of sympatric nesting raptors in the eastern deciduous forest biome. Canadian Journal of Zoology 70:984–992.

Capizzi, D., L. Caroli, and P. Varuzza. 1998. Feeding habits of sympatric Long-eared Owl *Asio otus*, Tawny Owl *Strix aluco* and Barn Owl *Tyto alba* in a Mediterranean coastal woodland. Acta Ornithologica 33:85–92.

Chiba, A., M. Onojima, and T. Kinoshita. 2005. Prey of the Long-eared Owl (*Asio otus*) in the suburbs of Niijata City, central Japan, as revealed by pellet analysis. Ornithological Science 4:169–172.

Cramp, S. and K. E. L. Simmons. 1985. Handbook of the birds of Europe, the Middle East, and North Africa. The birds of the Western Palearctic. Volume IV. Terns to woodpeckers. Oxford University Press, Oxford, United Kingdom.

Glue, D. E. and G. J. Hammond. 1974. Feeding ecology of the Long-eared Owl in Britain and Ireland. British Birds 67:361–369.

Jaffe, S. 1986. Climate of Israel. Pages 79–94 *in* The zoogeography of Israel (Y. Yom-Tov and E. Tchernov, Editors). W. Junk, Dordrecht, The Netherlands.

Marks, J. S. 1984. Feeding ecology of breeding Long-eared Owls in southwestern Idaho. Canadian Journal of Zoology 62:1528–1533.

Marti, C. D. 1974. Feeding ecology of four sympatric owls. Condor 76:45–61.

Marti, C. D. 1976. A review of prey selection by the Long-eared Owl. Condor 78:331–336.

Navarro, J., J. A. Sanchez-Zapata, M. Carrete, F. Botella, A. Gavrilov, S. Sklyarenoko, J. A. Donazar, O. Ceballos, and F. Hiraldo. 2003. Diet of three sympatric owls in steppe habitats of eastern Kazakhstan. Journal of Raptor Research 37:256–258.

Nilsson, I. N. 1981. Seasonal changes in food of the Long-eared Owl in southern Sweden. Ornis Scandinavica 12:216–223.

Paz, U. 1987. Birds of Israel. S. Steimatzky, Tel Aviv, Israel.

Raczyński, J. and A. L. Ruprecht. 1974. The effect of digestion on the osteological composition of owl pellets. Acta Ornithologica 14:25–37.

Shirihai, H. 1996. The birds of Israel. Academic Press, London, United Kingdom.

Tome, D. 1994. Diet composition of the Long-eared Owl in central Slovenia: seasonal variation in prey use. Journal of Raptor Research 28:253–258.

Village, A. 1981. The diet and breeding of Long-eared Owls in relation to vole numbers. Bird Study 28:215–224.

The Wilson Journal of Ornithology 120(3):645–648, 2008

First Observed Instance of Polygyny in Flammulated Owls

Brian D. Linkhart,[1,7] Erin M. Evers,[1,2] Julie D. Megler,[1,3] Eric C. Palm,[1,4] Catherine M. Salipante,[1,5] and Scott W. Yanco[1,6]

ABSTRACT.—We document the first observed instance of polygyny in Flammulated Owls (*Otus flammeolus*) and the first among insectivorous raptors. Chronologies of the male's two nests, which were 510 m apart, were separated by nearly 2 weeks. Each brood initially consisted of three owlets, similar to the mean brood size in monogamous pairs. The male delivered considerably fewer prey to the secondary nest, compared with prey-delivery rates at nests of monogamous males during the nestling period. Evidence suggested that all owlets fledged from the primary brood, but only one fledged from the secondary brood. We were uncertain of the cause of polygyny, but a possible explanation is the Hayman Fire shifted the operational sex ratio of the owls in favor of females. The extent of polygyny in Flammulated Owls may be limited by costs to the reproductive success of secondary females. *Received 10 February 2007. Accepted 22 December 2007.*

Facultative polygyny has been reported in nine species of strigiforms (Korpimäki 1983; Solheim 1983; Marti 1990; Marks et al. 1989, 1999, 2002), most of which feed primarily on small mammals. We document the first observed instance of polygyny in Flammulated Owls (*Otus flammeolus*), insectivores that feed primarily on moths (Reynolds and Linkhart 1987). This owl is a neotropical migrant, breeding in western North America and wintering as far south as Central America (McCallum 1994). Flammulated owls are cavity nesters and, in Colorado, breed in mature conifer forests dominated by ponderosa pine (*Pinus ponderosa*) (Linkhart 2001). The objective of this paper is to describe the polygynous event, and compare provisioning rates and fledging success at the male's two nests.

OBSERVATIONS

We initiated a study in 2003 of recolonization by Flammulated Owls of the area affected in the Hayman Fire, which burned the largest area (560 km^2) in recorded Colorado history in 2002 (Graham 2003). We located four territorial males in 2004, each of which occurred within a small parcel (20–30 ha) of unburned forest, and each separated by 7–20 km. One territorial male exhibited polygynous behavior, defined as a male feeding two females and their young at different nests at which no other male was detected. The two nests were 510 m apart, a distance somewhat greater than the mean (± SE) diameter of territories of monogamous males (428 ± 29 m; Linkhart 2001). We discovered the nests, both of which were in natural cavities in aspen (*Populus tremuloides*) trees, on 22 June (CS2 nest) and 12 July (CS1 nest) after hearing

[1] Department of Biology, Colorado College, 14 East Cache La Poudre Street, Colorado Springs, CO 80903, USA.

[2] 416 South Leyden Street, Denver, CO 80224, USA.

[3] 1 Alger Place, Grosse Pointe, MI 48230, USA.

[4] U.S. Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station, 505 Azuar Drive, Vallejo, CA 94592, USA.

[5] 94 Thornton Street, Hamden, CT 06517, USA.

[6] 154 Holliston Street, Medway, MA 02053, USA.

[7] Corresponding author; e-mail: blinkhart@coloradocollege.edu

adult feeding vocalizations near each nest. We captured and banded the CS2 female (USGS aluminum leg band #418) on 12 July, and the CS1 female (#381) on 13 July while each was day-roosting in her nest cavity. We captured the male with a small mist net (Reynolds and Linkhart 1984) on 15 July as he exited the CS1 nest at 1949 hrs MST and banded him (#419). We presumed he had delivered prey to the brooding CS1 female because his flight to the nest was preceded by food location calls, a distinctive sequence of behaviors shown by nesting males (Reynolds and Linkhart 1984). We captured the same male as he exited the CS2 nest at 2150 hrs following a presumed prey delivery. The male was not recaptured thereafter, but observations indicated he was the sole male tending the nests over the remainder of the nestling period. First, we observed only a banded male visiting the nests and the distance (7 km) to the nest of the closest banded male was sufficiently great (~6 times the maximum observed flight distance of radio-marked males; BDL, unpubl. data) that visits by other banded males were unlikely. Second, the male gave food location calls from the same particular perches near nests and we noted no deviations from this pattern that might suggest a second male. It also was unlikely a second male tended either nest prior to its discovery, since cooperative breeding is not known in this species (McCallum 1994).

Each brood initially consisted of three owlets, similar to the mean brood size in monogamous pairs (2.5 ± 0.1 owlets) (Linkhart and Reynolds 2006). We estimated, based on patterns of plumage development and mass gain in broods of monogamous pairs (BDL, unpubl. data), the CS1 owlets were 13, 17, and 18 days of age on 13 July, and the CS2 owlets were 1, 2, and 5 days of age on 12 July. Thus, the chronologies of the nests differed by nearly 2 weeks.

The male delivered considerably fewer prey to the secondary nest (CS2) during the nestling period compared with prey-delivery rates at nests of monogamous males. The male delivered 5.3 prey/hr (8 prey in 1.5 hrs) on one night (13 Jul) during the mid/latter portion of the nestling period at the CS1 nest, a somewhat lower rate than that by monogamous males at this time (8 prey/hr; Reynolds and Linkhart 1987). The male delivered 1.1 prey/hr (6 prey in 5 hrs) over three nights (12, 13, and 15 Jul) at the CS2 nest during the first week of the nestling period, which is much lower than by monogamous males at this time (7 prey/hr; Reynolds and Linkhart 1987). The male failed to deliver any prey to the CS2 nest in 2 hrs of observation on the last night of the nestling period (31 Jul). Each female delivered ≤2 prey/hr to her nest on the above nights, a similar rate to that of monogamous females (Reynolds and Linkhart 1987).

The evidence suggested that all owlets fledged from the CS1 nest, whereas only one fledged from the CS2 nest. The youngest owlet in the CS1 nest fledged on 20 July at ~20 days of age. We presume its two older siblings had fledged by this date, given that on 18 July the eldest owlet would have been ~23 days of age, which is the mean (± SD) duration (± 1 day) of the nestling period in Flammulated Owls (Reynolds and Linkhart 1987). It was unlikely the older siblings perished due to poor health, given that mass and feather development of each owlet on our previous visit (13 Jul) had been comparable to other owlets of similar age. In contrast, only the eldest owlet (#420) fledged from the CS2 nest at 23 days of age (30 Jul) when it had 24% less mass but similar primary development to other owlets at this age (n = 10; BDL, unpubl. data). The youngest owlet was missing when we visited the CS2 nest on 19 July and the second-eldest owlet was in poor condition, as indicated by having 42% less mass and a 70% shorter 5th primary feather compared to other 9-day old owlets (n = 18; BDL, unpubl. data). Two days later (21 Jul), we found the second-eldest owlet dead in the nest (specimen saved; BDL).

DISCUSSION

Our observations constitute the first reported instance of polygyny among insectivorous raptors. We were uncertain of its cause. One possible explanation is the Hayman Fire, which likely caused a significant loss of owl habitat (few trees, if any, survived in 51% of the forested area; Graham 2003), reduced the density of breeding males more than females, which are not territorial (Linkhart and Reynolds 2007). Polygyny occurred in passerines when the operational sex ratio shifted in favor of females (Greenlaw and Post 1985, Kempenaers 1994).

Polygyny has obvious potential benefits to the reproductive success of males, but the extent of polygyny among birds is believed to be most limited by costs to females (Orians 1969). Polygynous males often have reduced rates of provisioning at secondary nests compared to primary nests (Sejberg et al. 2000) with the possible consequence of reducing the reproductive success of secondary females (Johnson et al. 1993). Reduced provisioning by the male at the CS2 nest during the nestling period likely caused the mortality of two of the three owlets.

Reproductive success of female Flammulated Owls is particularly reliant on provisioning by males, not only because males provide most of the prey to nests during the nestling period, as is true with most owls (Marks et al. 1999), but also because most prey are small (~0.1 g) and are delivered singly to nests (Linkhart et al. 1998). Documenting mortality of nestling Flammulated Owls is uncommon in Colorado, as 95% (144 of 151) of banding-age owlets of monogamous males fledged from 1981 to 1999 (Linkhart 2001). Even more unusual is observing partial mortality within a brood, given there was just one other occasion when a portion of a brood died while the rest survived to fledge (n = 79; Linkhart 2001).

Polygyny in species with biparental care is more likely when chronologies of nesting cycles are staggered, according to the 'asynchronous-settlement model' (Leonard 1990), because of the difficulty of provisioning multiple nests when chronologies are similar (Johnson et al. 1993). A potential tradeoff of staggered nesting chronologies is that nestlings in secondary broods fledge at later dates, which may reduce survival rates of young in species such as Flammulated Owls that migrate long distances (Rappole 1995). Fledglings cannot forage independently of parents until 4–5 weeks after fledging (Linkhart and Reynolds 1987). Thus, owlet #420 could not have departed for migration before early September when arthropod prey becomes increasingly scarce in Colorado (BDL, unpubl. data). Owlets from only three broods (n = 132 broods) fledged at later dates than owlet #420 since 1981 (BDL, unpubl. data). This suggests there is strong selection against late fledging and, indirectly, against polygyny in this species.

ACKNOWLEDGMENTS

The authors thank C. E. Braun, J. S. Marks, and S. O. Williams III for helpful comments on the manuscript. We thank Colorado College, the Hulbert Center for Southwest Studies, the Hughes Undergraduate Research Program, the Lois Webster Fund (Audubon Society), and the USDA Forest Service for funding. The Rocky Mountain Research Station provided lodging.

LITERATURE CITED

Graham, R. T. (Editor). 2003. Hayman Fire case study. USDA, Forest Service, General Technical Report RM-114. Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Greenlaw, J. S. and W. Post. 1985. Evolution of monogamy in Seaside Sparrows, *Ammodramus maritimus*: tests of hypotheses. Animal Behaviour 33: 373–383.

Johnson, L. C., L. H. Kermott, and M. R. Lein. 1993. The cost of polygyny in the House Wren *Troglodytes aedon*. Journal of Animal Ecology 62: 669–682.

Kempenaers, B. 1994. Polygyny in the Blue Tit: unbalanced sex ratio and female aggression restrict male choice. Animal Behavior 47:943–957.

Korpimäki, E. 1983. Polygamy in Tengmalm's Owl *Aegolius funereus*. Ornis Fennica 60:86–87.

Leonard, M. L. 1990. Polygyny in Marsh Wrens: asynchronous settlement as an alternative to the polygyny-threshold model. American Naturalist 136:446–458.

Linkhart, B. D. 2001. Life history characteristics and habitat quality of Flammulated Owls (*Otus flammeolus*) in Colorado. Dissertation. University of Colorado, Boulder, USA.

Linkhart, B. D. and R. T. Reynolds. 1987. Brood division and postnesting behavior of Flammulated Owls. Wilson Bulletin 99:240–243.

Linkhart, B. D. and R. T. Reynolds. 2006. Lifetime reproduction of Flammulated Owls in Colorado. Journal of Raptor Research 40:29–37.

Linkhart, B. D. and R. T. Reynolds. 2007. Rate of return, fidelity, and dispersal in a breeding population of Flammulated Owls. Auk 124:264–275.

Linkhart, B. D., R. T. Reynolds, and R. A. Ryder. 1998. Home range and habitat of breeding Flammulated Owls in Colorado. Wilson Bulletin 110: 342–351.

Marks, J. S., R. J. Cannings, and H. Mikkola. 1999. Family Strigidae. Pages 76–151 *in* Handbook of the birds of the world. Volume 5 (J. del Hoyo, A. Elliott, and J. Sargatal, Editors). Lynx Editions, Barcelona, Spain.

Marks, J. S., J. L. Dickinson, and J. Haydock. 2002. Serial polyandry and alloparenting in Long-eared Owls. Condor 104:202–204.

Marks, J. S., J. H. Doremus, and R. J. Cannings. 1989. Polygyny in the Northern Saw-whet Owl. Auk 106:732–734.

MARTI, C. D. 1990. Same-nest polygyny in the Barn Owl. Condor 92:261–263.

MCCALLUM, A. 1994. Flammulated Owl (*Otus flammeolus*). The birds of North America. Number 93.

ORIANS, G. H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist 103:589–603.

RAPPOLE, J. H. 1995. The ecology of migrant birds: a neotropical perspective. Smithsonian Institutional Press, Washington, D.C., USA.

REYNOLDS, R. T. AND B. D. LINKHART. 1984. Methods and materials for capturing and monitoring Flammulated Owls. Great Basin Naturalist 44:49–51.

REYNOLDS, R. T. AND B. D. LINKHART. 1987. The nesting biology of Flammulated Owls in Colorado. Pages 239–248 *in* Biology and conservation of northern forest owls (R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, Editors). USDA, Forest Service, General Technical Report RM-142, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

SEJBERG, D., S. BENSCH, AND D. HASSELQUIST. 2000. Nestling provisioning in polygynous Great Reed Warblers (*Acrocephalus arundinaceus*): do males bring larger prey to compensate for fewer nest visits? Behavioral Ecology and Sociobiology 47: 213–219.

SOLHEIM, R. 1983. Bigyny and biandry in the Tengmalm's Owl (*Aegolius funereus*). Ornis Scandinavica 14:51–57.

The Wilson Journal of Ornithology 120(3):648–651, 2008

The Giant Hummingbird (*Patagona gigas*) in the Mountains of Central Argentina and a Climatic Envelope Model for its Distribution

Henrik von Wehrden[1,2]

ABSTRACT.—I present the first published observations of the Giant Hummingbird (*Patagona gigas*) in the mountains of central Argentina. This species was recorded in early and late summer 2006 and 2007. This new range resembles other summer habitats of the species, which are in the Andes >500 km distant. A climatic envelope model configured with known locations obtained from the literature predicts a high probability of occurrence in its "new" range. *Received 11 July 2007. Accepted 18 October 2007.*

The Giant Hummingbird (*Patagona gigas*) is the largest hummingbird in the world. Its distribution includes Ecuador (Ortiz-Crespo 1974, King and Holloway 1990), Colombia (Woods et al. 1998), Peru and Bolivia (Kokshaisky 2001, Wester and Classen-Bockhoff 2006), Chile (Vasquez and Simonetti 1999), and Argentina (Acreche et al. 1998, Osés 2003). This species typically inhabits high mountain habitats (Fjeldså and Krabbe 1990, Barnett and Pearmann 2001) and most records originate from the Andes. The altitudinal distribution of the species ranges to 4,600 m (Osés 2003) and is energy-driven (Fernandez and Bozinovic 2003). Narosky and Yzurieta (2003) indicate this species overwinters within the eastern lowlands of Argentina. However, all summer records originate from western Argentina in the vicinity of the Andes with important over-wintering habitats in north-western Argentina (Fjeldså and Krabbe 1990, Schuchmann 1999). A recent phylogenetic analysis of hummingbirds confirmed the species as being relatively isolated in relation to other hummingbird taxa (Altshuler et al. 2004). Osés (2003) classifies the species as comparatively primitive compared to other Trochilidae, which may be the reason for the variety of plants used by the taxon (Sahley 1996, Kokshaisky 2001, Schlumpberger and Badano 2005, Wester and Classen-Bockhoff 2006).

OBSERVATIONS

The Giant Hummingbird was encountered in the lower ranges of the Sierras Grandes de Córdoba, in central Argentina on 11 February 2006 at an altitude of ~1,430 m elevation (31° 40′ S, 64° 40′ W). The large size, char-

[1] Research Institute of Wildlife Ecology, Savoyen Strasse 1, 1160 Vienna, Austria.

[2] Institute of Biology, Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, 06099 Halle, Germany; e-mail: HenrikvonWehrden@web.de

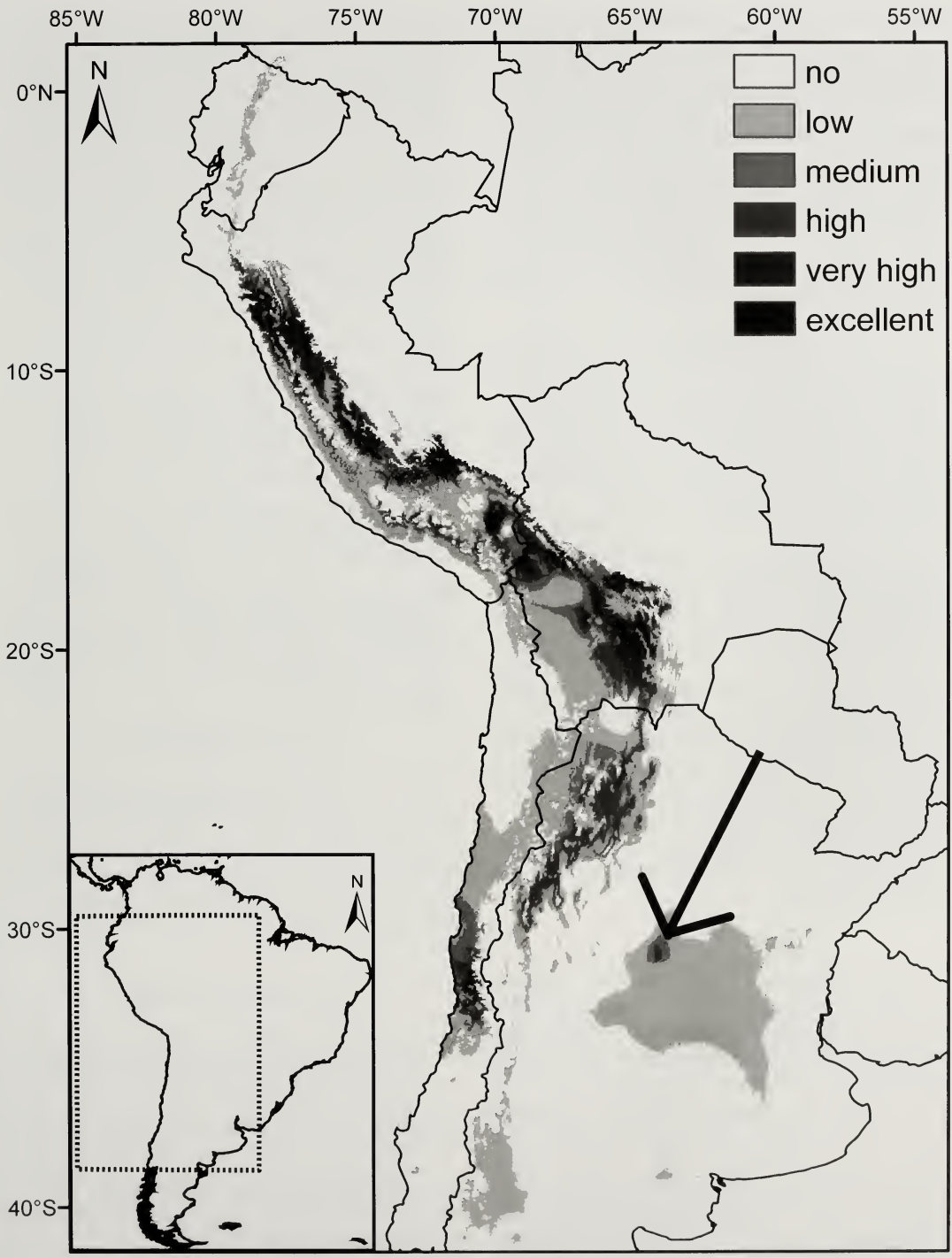


FIG. 1. Climatic envelope predicting distribution of the Giant Hummingbird in South America based on 99 known records. The arrow shows the area of the new records presented in this paper.

acteristic eye-ring, straight bill, and dull coloration made the identification definite (De La Pena and Rumboll 1998, Osés 2003). Further, the observed gliding flight is rather unusual within the Trochilidae. All other hummingbirds in the region are much smaller; the Red-tailed Comet (*Sappho sparganura*) was present, while the Blue-tufted Starthroat (*Heliomaster furcifer*) and the Glittering-bellied Emerald (*Chlorostilbon aureoventris*) were observed at lower altitudes and are easily distinguishable.

The Giant Hummingbird was encountered in the same location on 3 days during summer 2007 (18 and 19 Feb, 3 Apr) with multiple observations each day. The species was seen nine times by the author on the first day and confirmed by other scientists. The habitat was heterogeneous grassland, which contained some shrubs and a few trees (mainly *Maytenus boaria*). Several flowering plants represented potential feeding sources for the hummingbird, yet it was most often seen feeding on *Siphocampylus foliosus* (Campanulaceae). The hummingbird was observed at a distance of <3 m, hovering close to the observers on several occasions. The species was also seen at another location closer to the mountain range at a distance of 4 km (1,630 m elevation) from the first site. The birds were observed resting frequently in trees at both locations. Weather conditions were variable and observations were made on clear sunny and misty rainy days.

DISCUSSION

A spatial data base was created to construct a climatic envelope model for the species based on data obtained from Osés (2003). The new observations presented here were not incorporated into this model. Thus, a presence only model was created, which is a standard tool within ecological sciences (Peterson 2001, Pearce and Boyce 2006). Annual mean temperature, annual precipitation, mean temperature of the warmest quarter of the year, and annual temperature range were used as predictors and a public domain climate model (Hijmans et al. 2005) was used to derive the spatial model.

The model predicted the species with a high probability for the mountains of central Argentina, where I observed the species (arrow Fig. 1). I suggest the presence of the species in the area will be persistent since the species was present in both late and early summer over 2 years. The nearest known observations are from Salta (Acreche et al. 1998), San Juan (Contreras 1978), and Mendoza (Osés 2003) provinces, all of which are at a distance >500 km. The mountainous habitat where the observations were made resembles the known preference of the species, which is regarded to be selective for its habitat (Vasquez and Simonetti 1999). The observations support the unique island-like ecology of mountains of central Argentina (Nores 1995, Cabido et al. 1998). Thus, a permanent presence during the summer seems highly probable, which is also indicated by the climatic envelope model. The climatic distribution obtained from this model has a higher spatial resolution when compared to the standard literature. It demonstrates that climatic envelope models represent a valuable approach to identify the potential distribution of a species and helps researchers locate new distribution ranges. Model construction for other species might enhance our understanding of the distribution of these taxa as well.

ACKNOWLEDGMENTS

The author expresses gratitude to Heike Zimmermann and Heidi Hirsch for confirming his observation. Maurice Rumboll verified the record as new for the region. Danny McCluskey read earlier versions of this manuscript. Daniel Renison, C. E. Braun, and one anonymous referee provided helpful comments on the manuscript. The author thanks the Austrian Science Fund (Project P18624).

LITERATURE CITED

Acreche, N., H. A. Nunez, and M. V. Albeza. 1998. Vulnerabilidad de la avifauna en el Parque Nacional Los Cardones, Salta, Argentina. Revista de Biologia Tropical 46:811–816.

Altshuler, D. A., R. Dudley, and J. A. McGuire. 2004. Resolution of a paradox: hummingbird flight at high elevation does not come without a cost. Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences 101:17731–17736.

Barnett, J. M. and M. Pearmann. 2001. Annotated checklist of the birds of Argentina. Lynx Edicions, Barcelona, Spain.

Cabido, M., G. Funes, E. Pucheta, F. Vendramini, and S. Díaz. 1998. A chorological analysis of the mountains from central Argentina. Is all what we call Sierra Chaco really Chaco? Contribution to

the study of the flora and vegetation of the Chaco. XII. Candollea 53:321–331.

Contreras, J. 1978. Some comments on the races of the Giant Hummingbird, *Patagona gigas*, in the provinces of Mendoza and San Juan (Aves: Trochilidae). Neotropica 24:47–49.

De La Pena, M. R. and M. Rumboll. 1998. Birds of southern South America and Antarctica. Princeton University Press, Princeton, New Jersey, USA.

Fernandez, M. J. and F. B. Bozinovic. 2003. Flight efficiency and energetic costs along an altitudinal gradient in the world's largest hummingbird: *Patagona gigas*. Integrative and Comparative Biology 43:820.

Fjeldså, J. and N. Krabbe. 1990. Birds of the high Andes. Apollo books, Copenhagen, Denmark.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

King, J. R. and S. J. Holloway. 1990. Notes on the Giant Hummingbird *Patagona gigas* in southern Ecuador. Bulletin of the British Ornithologists Club 110:79–80.

Kokshaisky, N. V. 2001. Species composition, phenology and trophic relations in hummingbirds from Central Valley, Bolivia. Zoologichesky Zhurnal 80:210–221.

Narosky, T. and D. Yzurieta. 2003. Birds of Argentina and Uruguay. Vazquez Mazzini editores, Buenos Aires, Argentina.

Nores, M. 1995. Insular biogeography of birds on mountain-tops in north western Argentina. Journal of Biogeography 22:61–70.

Ortiz-Crespo, F. 1974. The Giant Hummingbird *Patagona gigas* in Ecuador. Ibis 116:347–359.

Osés, C. S. 2003. Taxonomy, phylogeny and biogeography of the Andean hummingbird Genera *Coeligena* LESSON, 1832; *Pterophanes* GOULD, 1849; *Ensifera* LESSON, 1843; and *Patagona* GRAY, 1840 (Aves: Trochiliformes). Dissertation. University of Bonn, Germany.

Pearce, J. L. and M. S. Boyce. 2006. Modeling distribution and abundance with presence-only data. Journal of Applied Ecology 43:405–412.

Peterson, A. T. 2001. Predicting species' geographic distributions based on ecological niche modeling. Condor 103:599–605.

Sahley, C. T. 1996. Bat and hummingbird pollination of an autotetraploid columnar cactus, *Weberbauerocereus weberbaueri* (Cactaceae). American Journal of Botany 83:1329–1336.

Schlumpberger, B. O. and E. I. Badano. 2005. Diversity of floral visitors to *Echinopsis atacamensis* ssp. *pasacana* (Cactaceae). Haseltonia 11:18–26.

Schuchmann, K.-L. 1999. Order Apodiformes. Family Trochilidae (Hummingbirds). Pages 468–535 *in* Handbook of the birds of the world. Volume 5. Barn-owls to hummingbirds (J. del Hoyo, A. Elliott, and J. Sargata, Editors). Lynx Edicions, Barcelona, Spain.

Vasquez, R. A. and J. A. Simonetti. 1999. Life history traits and sensitivity to landscape change: the case of birds and mammals of Mediterranean Chile. Revista Chilena de Historia Naturalista 72: 517–525.

Wester, P. and R. Classen-Bockhoff. 2006. Hummingbird pollination in *Salvia haenkei* (Lamiaceae) lacking the typical lever mechanism. Plant Systematics and Evolution 257:133–146.

Woods, S., F. Ortiz-Crespo, and P. M. Ramsay. 1998. Presence of Giant Hummingbird *Patagona gigas* and Ecuadorian Hillstar *Oreotrochilus chimborazo jamesoni* at the Ecuador-Colombia border. Cotinga 10:37–40.

The Wilson Journal of Ornithology 120(3):651–653, 2008

Giant Hummingbirds (*Patagona gigas*) Ingest Calcium-rich Minerals

Cristián F. Estades,[1,2] M. Angélica Vukasovic,[1] and Jorge A. Tomasevic[1]

ABSTRACT.—We report Giant Hummingbirds (*Patagona gigas*), regularly and deliberately, ingesting wood ashes and slaked lime in central Chile. These two minerals have high concentrations of calcium, which may be a scarce element in the nectar-based diet of the species. Both observations occurred during the post-breeding period suggesting the birds were females ingesting calcium-rich compounds to replace minerals lost during eggshell production. *Received 31 March 2007. Accepted 10 November 2007.*

[1] Laboratorio de Ecología de Vida Silvestre, Departamento de Manejo de Recursos Forestales, Universidad de Chile, Casilla 9206, Santiago, Chile.

[2] Corresponding author; e-mail: cestades@uchile.cl

The nectar-based diet of hummingbirds poses nutritional restrictions such as a limited

supply of proteins and some minerals. These nutrients are usually obtained from insects that hummingbirds include in their diet (Remsen et al. 1986). However, minerals may be lost at a much higher rate through the highly diluted urine of hummingbirds, or during egg production (Adam and des Lauriers 1998). The latter may cause hummingbirds to supplement their diet with mineral-rich compounds (Adam and des Lauriers 1998). We report two different observations of the Giant Hummingbird (*Patagona gigas*) deliberately ingesting calcium-rich minerals in central Chile.

OBSERVATIONS

We observed an adult Giant Hummingbird on several occasions during February 2005 (austral summer) visit a site where ashes from a barbecue had accumulated on the ground at the Pantanillos Forest Research Station (35° 32′ S, 72° 17′ W) near Constitución in central Chile. Our first impression was the bird was looking for insects but we soon realized it was apparently ingesting ashes. Each time the bird would sit on the ground and place its beak into the soil or at a short distance above the ground while licking the ashes with its tongue. The bird came to the site regularly, making 2–3 short visits (<2 min) during the morning (0800–1000 hrs) and afternoon (1700–1800 hrs).

MAV observed an adult Giant Hummingbird during most of February 2007 coming regularly to a wall of an old country house painted with slaked lime (calcium hydroxide) near the town of Quirihue (36° 20′ S, 72° 38′ W) in central Chile. The bird flew directly to two different spots in the wall where lime dust accumulated inside small crevices. At the spot closer to the ground (0.3 m) the bird would hover while licking the wall, whereas at the higher location (1.7 m) the bird would usually sit while reaching inside the crevice with its beak. Close inspection of these crevices failed to detect the presence of insects, spider webs or other nest building materials, which could be attracting the birds. The bird visited the site in the morning and in the afternoon, but made only one visit at each time of the day.

DISCUSSION

Calcium is one of the main components of wood ashes (des Lauriers 1994) and the slaked lime dust, although probably mixed with dirt, was likely rich in calcium as well. We believe the observed birds were regularly and deliberately ingesting calcium-rich compounds.

We could not identify the gender of the birds because the Giant Hummingbird is sexually monochromatic with males and females differing only slightly in size (Araya et al. 1986). This is important because most records of hummingbirds ingesting calcium are of females (Verbeek 1971, des Lauriers 1994, Adam and des Lauriers 1998) that are likely trying to meet their requirements of calcium for eggshell production.

Our observations likely corresponded to birds in the post-breeding period as nesting for this species in this region normally occurs between October and January (pers. obs.). We cannot completely eliminate the possibility the birds were late breeders because, unfortunately, we did not look for nests. However, we doubt the latter was the case because the species migrates from the region in March.

It is believed that hummingbirds, being the smallest birds alive, do not have sufficient medullary bone for storing calcium for eggshell production (Adam and des Lauriers 1998). Ingestion of extraneous calcium by birds that cannot store calcium in medullary bones should peak near the period of maximum breeding activity (Dhondt and Hochachka 2001). Our observations suggest that Giant Hummingbirds were ingesting minerals to replace the calcium lost during eggshell production that had likely occurred 2–3 months earlier. It is possible the Giant Hummingbird, being four times heavier (18–22 g) than most hummingbird species (3–5 g), has a higher calcium storage capacity.

Ours are not the only observations of hummingbirds ingesting calcium after the breeding period. Verbeek (1971) reported a female Anna's Hummingbird (*Calypte anna*) feeding on calcium-rich sand more than a month after the last reported date for a clutch of the species. Most records of female hummingbirds apparently taking calcium are from the nesting period (des Lauriers 1994, Adam and des Lauriers 1998), including several Anna's Hummingbirds (Adam and des Lauriers 1998). We did not observe consumption of calcium by Giant Hummingbirds when nests are active

(Oct–Nov) during several years of work in both field sites.

Hummingbirds have been reported eating calcium-rich sand and soil (Verbeek 1971, Adam and des Lauriers 1998). Ash-eating behavior had been previously described for some North American hummingbirds (des Lauriers 1994) but, to our knowledge, there are no reports of this behavior for the Giant Hummingbird or any other hummingbird in the Southern Hemisphere. We believe the record of the consumption of slaked lime is the first for a hummingbird, and probably the second for a bird, after the observation reported by Richmond (1953) of Purple Martins (*Progne subis*) ingesting slaked lime from the ground in Oregon.

ACKNOWLEDGMENTS

We appreciate the comments of two anonymous referees.

LITERATURE CITED

Adam, M. A. and J. R. des Lauriers. 1998. Observations of hummingbirds ingesting mineral-rich compounds. Journal of Field Ornithology 69:257–261.

Araya, B., G. Millie, and M. Bernal. 1986. Guía de Campo de las Aves de Chile. Editorial Universitaria, Santiago, Chile.

des Lauriers, J. R. 1994. Hummingbirds eating ashes. Auk 111:755–756.

Dhondt, A. A. and W. M. Hochachka. 2001. Variations in calcium use by birds during the breeding season. Condor 103:592–598.

Remsen Jr., J. V., F. G. Stiles, and P. E. Scott. 1986. Frequency of arthropods in stomachs of tropical hummingbirds. Auk 103:436–441.

Richmond, S. M. 1953. The attraction of Purple Martins to an urban location in western Oregon. Condor 55:225–249.

Verbeek, N. A. M. 1971. Hummingbirds feeding on sand. Condor 73:112–113.

The Wilson Journal of Ornithology 120(3):653–654, 2008

Nocturnal Foraging Observations of the Blue-crowned Motmot (*Momotus momota*) in San José, Costa Rica

Alejandro Solano-Ugalde[1,2] and Agustina Arcos-Torres[1]

ABSTRACT.—We provide documentation on the first observations of nocturnal foraging by the Blue-crowned Motmot (*Momotus momota*). The motmot we observed mainly fed on sphinx (Sphingidae) moths; the capture rate seemed low for this fairly large prey. *Received 27 April 2007. Accepted 26 October 2007.*

Nocturnal foraging has only been reported once (Thurber and Komar 2002) for the neotropical Momotidae: Coraciformes, despite many hours of field observations (Skutch 1945, 1947, 1964, 1971; Orejuela 1980, Remsen et al. 1993, Chacón-Madrigal and Barrantes 2004, Garcia-C and Zahawi 2006). The Thurber and Komar (2002) report involved a single Turquoise-browed Motmot (*Eumomota superciliosa*) in the Republic of El Salvador, which for 2 consecutive years (1975–1976) fed on insects attracted to an artificial light source in a residential yard. We provide documentation in this note of the first known observations of nocturnal foraging by the Blue-crowned Motmot (*Momotus momota*).

OBSERVATIONS

We report opportunistic observations of a single Blue-crowned Motmot nocturnally foraging on aerial insects in the vicinity of an electric street lamp at Coopecabañas, San José, Costa Rica (09° 55′ N, 84° 12′ W; 910 m elevation). Our first observation was on 5 December 2004 at 2128 hrs when we observed a motmot on the lawn of a residence feeding on a fairly large sphinx moth (Sphingidae). The bird perched 2 m above the ground, after

[1] Fundación Imaymana, Lincoln 199 y San Ignacio, Quito, Ecuador.

[2] Corresponding author; e-mail: jhalezion@gmail.com

consuming the moth, on an almost vertical branch of a fallen tree in the hilly terrain next to the artificial light source. This perch seemed to provide the bird with cover from direct light while allowing an ample vantage point. The observed bird performed five successful foraging sallies in 30 min of observation; all captured prey appeared to be sphinx moths. On two other occasions, we found presumably the same bird feeding near the same street light: 18 December 2004 and 1 January 2005. The bird used the same foraging method each time, usually sallying upwards or horizontally from its perch to attempt prey capture. Only on two occasions did the motmot succeed in direct aerial capture. In the remaining foraging attempts (40), it had problems capturing prey in the air and usually would have a vertical downward chase to the lawn, where it occasionally succeeded and proceeded with feeding. We checked the area during six nights in August 2006 but did not find any motmots feeding in the area.

The inferred capture efficiency was quite low. However, the large size of prey may compensate, as we observed the motmot did not need many feeding events to be apparently satiated as it left the scene. The capture rate could reflect the lack of adaptative response, which a more specialized bird would have to couple with its new foraging behavior.

Artificial lights and motmots are common in suburbs around San Jose and other nearby Costa Rican provinces. However, diurnal insectivorous birds attracted to artificial light sources during the night have not previously been recorded for Costa Rica.

ACKNOWLEDGMENTS

We thank Julio Sánchez and Gilbert Barrantes for encouraging preparation of this note. We also thank Christopher Canaday, Oliver Komar, and an anonymous reviewer for helpful comments which greatly improved this manuscript.

LITERATURE CITED

Chacón-Madrigal, E. and G. Barrantes. 2004. Blue-crowned Motmot (*Momotus momota*) predation on a long-tongued bat (Glossophaginae). Wilson Bulletin 116:108–110.

Garcia-C, J. M. and R. A. Zahawi. 2006. Predation by a Blue-crowned Motmot (*Momotus momota*) on a hummingbird. Wilson Journal of Ornithology 118:261–263.

Orejuela, J. 1980. Niche relationships between Turquoise-browed and Blue-crowned motmots in the Yucatan Peninsula, Mexico. Wilson Bulletin 92: 229–244.

Remsen, J. V., M. Hyde, and A. Chapman. 1993. The diets of neotropical trogons, motmots, barbets and toucans. Condor 95:178–192.

Skutch, A. 1945. Life history of the Blue-throated Green Motmot. Auk 62:489–517.

Skutch, A. 1947. Life history of the Turquoise-browed Motmot. Auk 64:201–217.

Skutch, A. 1964. Life history of the Blue-diademed Motmot *Momotus momota*. Ibis 106:321–332.

Skutch, A. 1971. Life history of the Broad-billed Motmot, with notes on the Rufous Motmot. Wilson Bulletin 83:74–94.

Thurber, W. A. and O. Komar. 2002. Turquoise-browed Motmot (*Eumomota superciliosa*) feeds by artificial light. Wilson Bulletin 114:525–526.

The Wilson Journal of Ornithology 120(3):655–657, 2008

Kleptoparasitism by Grey Kingbirds (*Tyrannus dominicensis*) in Barbados

Sarah E. Overington,[1,2] Laure Cauchard,[1] and Kimberly-Ann Côté[1]

ABSTRACT.—We observed Grey Kingbirds (*Tyrannus dominicensis*) from late February to May 2007 stealing food items from the bills of Carib Grackles (*Quiscalus lugubris*). This behavior occurred at two baited walk-in bird traps on the grounds of Bellairs Research Institute of McGill University in St James, Barbados. Grey Kingbirds were not seen entering traps, but were regularly observed in tree branches near traps, often chasing Carib Grackles and Zenaida Doves (*Zenaida aurita*) as they exited the traps with food. We describe six instances of kleptoparasitism by Grey Kingbirds from Carib Grackles. To our knowledge, this is the first report of kleptoparasitism for this species. *Received 18 July 2007. Accepted 30 December 2007.*

The Grey Kingbird (*Tyrannus dominicensis*) is a mid-sized tyrant flycatcher found throughout the Caribbean, northern South America, and into southern North America (Smith and Jackson 2002). Its diet consists of insects, lizards, berries, fruits, and seeds (Smith and Jackson 2002), but it has also been observed at food scrap assemblages in Barbados (Lefebvre et al. 2001). Grey Kingbirds hunt using a typical flycatcher technique, descending from high perches to capture prey in mid-air (Smith and Jackson 2002). They may also take insects from the surface of water (Sprunt 1942, Lack 1976), capture fish in shallow water and sand bars (Lefebvre and Spahn 1987), and have occasionally been observed feeding at night near lights and street lamps (Reader et al. 2002). Grey Kingbirds are noted for their aggression toward mammals and other birds, particularly during the breeding season as they defend their nests (Sprunt 1942). However, no cases of aggressive behavior involving food theft (kleptoparasitism; Brockmann and Barnard 1979) have been described for this species and only a single case of kleptoparasitism has been reported for the genus (i.e., Cassin's Kingbird [*T. vociferans*] stealing worms from "Blackbirds"; Merriam 1896). No reports of kleptoparasitism by Grey Kingbirds were found in a recent exhaustive survey covering 856 field reports of kleptoparasitism in birds published since 1969 (Morand-Ferron et al. 2007).

[1] Department of Biology, McGill University 1205 Avenue Docteur Penfield, Montreal, QC H3A 1B1, Canada.

[2] Corresponding author; e-mail: sarah.overington@mail.mcgill.ca

OBSERVATIONS

We observed six acts of interspecific kleptoparasitism by Grey Kingbirds from late February to May 2007 at the Bellairs Research Institute of McGill University in St James, Barbados. All kleptoparasitic attacks occurred near two walk-in traps (1 × 0.55 × 0.55 m) on the grounds of the research institute (13° 10′ 60 N, 59° 38′ 60 W). These traps were made of wire affixed to a wooden frame, and we baited them regularly with moistened dog food pellets and cooked rice. We placed food near the back of the traps so that birds had to move at least 30 cm into a trap to reach the bait, because this increased our success in capturing our target species, Carib Grackles (*Quiscalus lugubris*). The two traps had the same dimensions, but were ~200 m apart, separated by a large building. One was closer to the front entrance of the research institute and we refer to this as the "front trap" with the other being the "back trap". Each trap was within 5 m of trees where Grey Kingbirds were seen perching.

On 19 February 2007 at 1723 hrs AST, we saw a Grey Kingbird descend from a tree branch above the front trap and, in mid-flight, steal a moistened dog food pellet from the bill of an adult Carib Grackle that was walking out of the trap. On 17 March 2007, a Grey Kingbird descended from a tree above the back trap and stole food from an adult Carib Grackle without landing on the ground. On 21 March at 850 hrs, a Grey Kingbird stole a dog food pellet from the bill of an adult female Carib Grackle at the front trap. Between 1240

and 1250 hrs, we observed two acts of kleptoparasitism at the back trap. First, a Grey Kingbird stole a dog food pellet from a Carib Grackle without landing on the ground. Second, a Carib Grackle released a dog food pellet from its bill as a Grey Kingbird descended from the tree and the Grey Kingbird took the pellet from the ground. On 23 April at 1446 hrs, we observed a different kleptoparasitic technique at the back trap where a Grey Kingbird chased a Carib Grackle and stole a dog food pellet while both birds were in flight. Kleptoparasitism was observed several times by other researchers at both traps until they were removed from the research grounds on 21 May 2007, but the details of these observations were not recorded.

Two Grey Kingbirds were often observed together around the research institute and near the traps, although they were not observed stealing food at the same time. All birds we observed stealing food had adult plumage. We were unable to identify males from females by sight, although Grey Kingbirds show some sexual size dimorphism (Haberman et al. 1991). None of the kleptoparasitizing individuals had any obvious features that would allow us to distinguish between them and we cannot be sure of the number of individuals engaging in kleptoparasitism. Grey Kingbirds were regularly seen in trees near the traps throughout the trapping period (Feb–May 2007), but were not observed entering either trap and were rarely seen on the ground. Grey Kingbirds often arrived shortly after the traps had been baited and were observed chasing both Zenaida Doves (*Zenaida aurita*) and Carib Grackles from the trap area on at least four occasions in what appeared to be failed attempts to steal food.

DISCUSSION

Animals may steal food to gain access to items that would otherwise be difficult to acquire due to morphological or behavioral constraints. For example, juvenile Eurasian Oystercatchers (*Haematopus ostralegus*) reduce their rates of stealing mussels (*Mytilus edulis*) from adult conspecifics as they become more efficient at opening the mussel shells (Goss-Custard et al. 1998). Even if a species is capable of performing difficult foraging tasks, kleptoparasitism may allow it to access food items at a lower cost. Food stealing by gulls (Laridae) allows them to obtain foods such as fish (Duffy 1980), mussels (Khatchikian et al. 2002), and refuse (Burger and Gochfeld 1976) without performing the diverse foraging techniques required to access these items (e.g., diving, cracking open hard shells, digging). This may also be the case for the Grey Kingbirds we observed. The design and dimensions of our walk-in traps made it impossible for individuals to retrieve dog food pellets using their usual in-flight foraging strategy. Consequently, kleptoparasitism represented an alternative foraging strategy for these birds, allowing them to access a valuable (protein-rich) food source.

The Grey Kingbird is a territorial species that aggressively chases other birds and mammals from nesting areas. The food stealing and chasing we observed may be a modification of existing foraging behavior as well as agonistic behavior toward other birds within the breeding territory. There was a Grey Kingbird nest within 50 m of one of the two traps where we observed kleptoparasitic behavior, although we could not confirm this nest belonged to the individuals engaged in food stealing. No studies have been conducted on the population of Grey Kingbirds at this location and we cannot speculate on territory size or whether individuals stealing food were territory owners.

Our research group has been trapping birds at Bellairs Research Institute for several decades, but neither stealing nor eating of dog food pellets by Grey Kingbirds have been observed before (Louis Lefebvre, pers. comm.). Our repeated observations suggest that food stealing is an opportunistic foraging technique used by at least one individual at our field site. Opportunistic feeding behavior may contribute to the success of the Grey Kingbird in Barbados, an island dominated by human-modified habitats.

ACKNOWLEDGMENTS

We thank the staff at Bellairs Research Institute for their support and encouragement. Comments from P. A. Buckley and an anonymous reviewer improved the manuscript greatly. We thank Julie Morand-Ferron, Louis Lefebvre, and Neeltje Boogert for helpful comments on a previous version of this work. This research was funded by NSERC through a graduate fellowship to SEO and a Discovery grant to Louis Lefebvre.

LITERATURE CITED

Brockmann, H. J. and C. J. Barnard. 1979. Kleptoparasitism in birds. Animal Behaviour 27:487–514.

Burger, J. and M. Gochfeld. 1976. Age differences in Ring-billed Gull kleptoparasitism on starlings. Auk 96:806–808.

Duffy, D. C. 1980. Patterns of piracy by Peruvian seabirds. Ibis 122:521–525.

Goss-Custard, J. D., J. T. Cayford, and S. E. G. Lea. 1998. The changing trade-off between food finding and food stealing in juvenile oystercatchers. Animal Behaviour 55:745–760.

Haberman, K., D. I. MacKenzie, and J. D. Rising. 1991. Geographic variation in the Gray Kingbird. Journal of Field Ornithology 62:117–131.

Khatchikian, C. E., M. Favero, and A. I. Vassallo. 2002. Kleptoparasitism by Brown-hooded Gulls and Grey-hooded Gulls on American Oystercatchers. Waterbirds 25:137–141.

Lack, D. 1976. Island biology: illustrated by the land birds of Jamaica. University of California Press, Berkeley, USA.

Lefebvre, L. and D. Spahn. 1987. Gray Kingbird predation on small fish (*Poecilia* sp.) crossing a sandbar. Wilson Bulletin 99:291–292.

Lefebvre, L., S. Reader, and S. J. Webster. 2001. Gray Kingbirds join a bread scrap assemblage in Barbados. Bulletin of Ornithology 1211:247–249.

Merriam, F. A. 1896. Notes of some of the birds of Southern California. Auk 13:115–124.

Morand-Ferron, J., D. Sol, and L. Lefebvre. 2007. Food-stealing in birds: brain or brawn? Animal Behaviour 74:1725–1734.

Reader, S. M., J. Morand-Ferron, I. Côté, and L. Lefebvre. 2002. Unusual feeding behaviors in five species of Barbadian birds. El Pitirre 15:117–123.

Smith, G. A. and J. A. Jackson. 2002. Gray Kingbird (*Tyrannus dominicensis*). The birds of North America. Number 668.

Sprunt Jr., A. 1942. *Tyrannus dominicensis dominicensis* (Gmelin) Gray Kingbird. Pages 29–50 *in* Life histories of North American flycatchers, larks, swallows, and their allies (A. C. Bent, Editor). U.S. National Museum Bulletin Number 179.

The Wilson Journal of Ornithology 120(3):657–659, 2008

Double-scratching by Yellow-headed Blackbirds

Alan de Queiroz[1]

ABSTRACT.—Some ground-foraging birds, including most New World sparrows in the tribe Emberizini, uncover food items in litter by double-scratching, a backward hop that displaces the litter posteriorly. I report double-scratching by Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), a species not previously known to exhibit this behavior. Double-scratching by one individual that was observed in detail occurred with the bill pointed downward with its tip near or touching the ground, as in other icterines but unlike the behavior in Emberizini. This individual, between double-scratches, also used bill-sweeping to displace litter. Double-scratching has a similar form in at least three of the four icterine species reported to show the behavior, suggesting the trait is homologous among these species. However, phylogenetic relationships imply that double-scratching evolved convergently in these taxa. *Received 6 June 2007. Accepted 5 January 2008.*

A number of ground-foraging birds use a distinctive double-scratching behavior to uncover food items under litter or other material. Double-scratching, or bilateral scratching (Greenlaw 1976, 1977), refers specifically to synchronous movement of both legs to scratch away surface material, as opposed to using one leg at a time. This behavior typically involves a forward hop immediately followed by a backward hop (the scratching stroke) that displaces litter posteriorly (Harrison 1967; Greenlaw 1976, 1977).

Double-scratching is especially widespread in New World sparrows of the tribe Emberizini and seems to occur in few species outside of this group (Davis 1957; Harrison 1967; Greenlaw 1976, 1977; Hailman 1984; Whalen and Watts 2000; [taxonomy follows Klicka et al. 2000]). Among icterines, double-scratching has been reported for only three species—Red-winged Blackbird (*Agelaius phoeniceus*),

[1] 826 Delmar Way, Reno, NV 89509, USA; e-mail: alandqz@yahoo.com

Brown-headed Cowbird (*Molothrus ater*), and Shiny Cowbird (*M. bonariensis*) (Greenlaw 1976). Red-winged Blackbirds and Brown-headed Cowbirds apparently use the behavior somewhat commonly (Greenlaw 1976).

I report double-scratching by Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), a species distantly related to other icterines known to show this behavior (Lanyon and Omland 1999, Jønsson and Fjeldså 2006), and briefly discuss the phylogenetic history of the behavior within Icterini. I also report a Yellow-headed Blackbird alternately using double-scratching and bill-sweeping on the same substrate, a specific combination of behaviors that apparently has not been reported previously in any bird species.

OBSERVATIONS

Birds were observed in a yard in Ely, White Pine County, Nevada, USA (39° 13′ 30.5″ N, 114° 52′ 19.5″ W). On the afternoon of 6 May 2007, a large flock of Brown-headed Cowbirds and at least four Yellow-headed Blackbirds flew into the yard and fed on bird seed (a mix of millet, cracked corn, and sunflower seeds) that had been cast onto the lawn and into a shrub bed covered with bark (mostly pieces <1 cm wide by 2 cm long). Many of the cowbirds and at least two of the Yellow-headed Blackbirds double-scratched in the shrub bed to displace the bark and uncover the seeds.

I watched an immature male Yellow-headed Blackbird from 1610 to 1615 hrs PST on 6 May perform at least a dozen double-scratches in the shrub bed. In double-scratching, the bird made a forward hop immediately followed by a backward hop. The legs of the bird were usually offset at the beginning of the double-scratch (i.e., one leg was farther forward than the other) and this offset position at times remained at the end of the backward hop. The movements of the two legs did not seem to be perfectly synchronous in some instances, although evaluating synchrony was difficult. The blackbird's double-scratching movements were clearly slower than those of cowbirds, a Green-tailed Towhee (*Pipilo chlorurus*), and several White-crowned Sparrows (*Zonotrichia leucophrys*) that were also feeding in the shrub bed on the same afternoon. All of these species also fed on the lawn, but only the Green-tailed Towhee was observed double-scratching on that substrate.

I watched an adult male Yellow-headed Blackbird feeding in the same shrub bed from ~1310 to ~1340 hrs PST on 8 May 2007. I focused my observations of 8 May on the positions of the bill and legs. This adult male kept its head pointed downward with the tip of the bill touching or nearly touching the ground while double-scratching. The legs of the bird were at times obviously splayed at the end of a double-scratch. The backward hop propelled bark or other litter behind the bird and the wings of the bird were at times held slightly away from the body. As on 6 May, I had the impression the bird did not always move its legs synchronously while double-scratching.

I performed a timed 5-min watch of this bird from 1334 to 1339 hrs to obtain a sample of the frequency of double-scratching while the bird was feeding continuously. The bird double-scratched four times during this period and also, from a position with the bill tip touching or nearly touching the substrate, swept its bill upwards many times with both a forward and a lateral component. These bill-sweeping movements also displaced litter.

DISCUSSION

This report, to my knowledge, represents the first published record of double-scratching by Yellow-headed Blackbirds. This behavior in this species appears to be similar to that reported by Greenlaw (1976) for Red-winged Blackbirds and Brown-headed Cowbirds. These three icterine species hold the bill pointing downward with the tip near or touching the substrate and they often end the backward hop with legs splayed. All three may also move the legs asynchronously (although this needs to be verified for Yellow-headed Blackbirds). The position of the bill during double-scratching is clearly different from that in New World sparrows (Emberizini), which typically double-scratch with the bill held well above the substrate (Greenlaw 1976). The splayed legs and asynchronous leg movements may also distinguish icterine double-scratching from that of most members of the Emberizini, although some species in the latter group show these characteristics in some circumstances (Greenlaw 1976).

The positions of the head and legs suggest the trait is homologous in the three double-scratching icterine species (Red-winged Blackbird, Brown-headed Cowbird, Yellow-headed Blackbird) for which the behavior has been described in detail. However, estimates of phylogenetic relationships within the icterines (Lanyon and Omland 1999, Jønsson and Fjeldså 2006) suggest double-scratching has evolved independently in these three taxa. One explanation for this apparent contradiction is that double-scratching may be present but unreported in other icterine species. The assumption is that, if the taxonomic distribution of double-scratching was more accurately known, phylogenetic analyses would show the trait has arisen only once within the group. This explanation seems plausible considering that, until the 1970s, double-scratching had been reported in only one icterine species, the Shiny Cowbird. It is now known to occur in three other common and conspicuous species within this group (Greenlaw 1976, this study). Observations of other icterine species feeding in conditions that might elicit double-scratching would help clarify this issue. Red-winged Blackbirds, Brown-headed Cowbirds, and Yellow-headed Blackbirds have all been observed double-scratching in bark litter (Greenlaw 1976, this study) suggesting one context in which the behavior might be observed in other icterines.

The alternating use of double-scratching and bill-sweeping on the same substrate apparently has not been reported previously for any bird species. Other species are known to use both double-scratching and bill-sweeping to move litter or other material, but not in the manner described in this paper. Egyptian Plovers (*Pluvianus aegyptius*) use both behaviors, but in different feeding contexts (Howell 1979). Some species of brush finches (*Atlapetes*) also double-scratch and bill-sweep, but it is unclear whether individual birds use both behaviors (Paynter 1978). Three thrush (*Turdus*) species are known to double-scratch simultaneously with bill-sweeping (Clark 1983). An obvious question concerning Yellow-headed Blackbirds is whether switching from one behavior to the other is tied to some subtle difference in context, such as small differences in the size of pieces of litter.

ACKNOWLEDGMENTS

I thank M. C. Witmer and T. A. Forbis for helpful comments on the manuscript and M. C. Witmer for references on Yellow-headed Blackbirds.

LITERATURE CITED

Clark Jr., G. A. 1983. An additional method of foraging in litter by species of *Turdus* thrushes. Wilson Bulletin 95:155–157.

Davis, J. 1957. Comparative foraging behavior of the Spotted and Brown towhees. Auk 74:129–166.

Greenlaw, J. S. 1976. Use of bilateral scratching behavior by emberizines and icterids. Condor 78: 94–97.

Greenlaw, J. S. 1977. Taxonomic distribution, origin, and evolution of bilateral scratching in ground-feeding birds. Condor 79:426–439.

Hailman, J. P. 1984. Effect of litter on leaf-scratching emberizines. Wilson Bulletin 96:121–125.

Harrison, C. J. O. 1967. The double-scratch as a taxonomic character in the Holarctic Emberizinae. Wilson Bulletin 79:22–27.

Howell, T. R. 1979. Breeding biology of the Egyptian Plover, *Pluvianus aegyptius*. University of California Publications in Zoology 113:1–76.

Jønsson, K. A. and J. Fjeldså. 2006. A phylogenetic supertree of oscine passerine birds (Aves: Passeri). Zoologica Scripta 35:149–186.

Klicka, J., K. P. Johnson, and S. M. Lanyon. 2000. New World nine-primaried oscine relationships: constructing a mitochondrial DNA framework. Auk 117:321–336.

Lanyon, S. M. and K. E. Omland. 1999. A molecular phylogeny of the blackbirds (Icteridae): five lineages revealed by cytochrome-*b* sequence data. Auk 116:629–639.

Paynter Jr., R. A. 1978. Biology and evolution of the genus *Atlapetes* (Emberizinae). Bulletin of the Museum of Comparative Zoology 148:323–369.

Whalen, D. M. and B. D. Watts. 2000. Interspecific variation in extraction of buried seeds within an assemblage of sparrows. Oikos 88:574–584.

The Wilson Journal of Ornithology 120(3):660–665, 2008

Ornithological Literature

Compiled by Mary Gustafson and Clait E. Braun

THE ORNITHOLOGIST'S DICTIONARY. By Johannes Erritzoe, Kaj Kampp, Kevin Winker, and Clifford B. Frith. Lynx Edicions, Barcelona, Spain. 2007: 284 pages. ISBN: 9788496553439. $25.00 (paper).—Lynx Edicions, based in Barcelona, Catalonia, are best-known to birdwatchers and ornithologists as publishers of the monumental "*Handbook of the Birds of the World*", but their range in bird-related works is large and growing with numerous new titles in English, Spanish, and (I am glad to say) Catalan appearing every year. This latest work is another useful addition to their catalogue.

As the name suggests, this is specifically a dictionary. Aside from a six-page appendix listing bird families with the number of species in each, the entire book is devoted to an alphabetic treatment of some 5,000 words and terms. Each entry is terse and to-the-point; this is not a collection of essays, but a collection of definitions and facts, expressed as concisely as possible. The authors seem to have gone out of their way to make their selection varied and encompassing, including such disparate items as non-obvious abbreviations, such as *per se* and *incertae sedis*, ornithological societies and publications, behavior patterns, bird diseases, a few of the more outstanding luminaries of biology such as Darwin and Linnaeus, anatomical terms, Malaysian mythology, advances in nucleic acid science, important fossils, some obscure words to describe habitats, etc. The net is cast very widely indeed.

The similarity between the titles invites an obvious comparison between the present work and Sir Arthur Landsborough Thomson's classical "*A New Dictionary of Birds*" published more than 40 years ago, but this is scarcely a valid comparison. The "New Dictionary" was in fact more in the nature of an encyclopedia rather than what most people would understand as a dictionary with essays, rather than entries, contributed by some 200 distinguished scientists, and with numerous illustrations, photographs, and color plates, in more than 900 large-format pages. "The Ornithologist's Dictionary" is precisely that, a far more concise venue for laconically-expressed facts and definitions, with the artwork confined to one little vignette at the head of each letter of the alphabet.

How well does "The Ornithologist's Dictionary" fulfill its objectives? In short, I think very well. Obviously, a determined reviewer with an obsession for nit-picking could comment on omissions—among the publications, "*Birds of the Western Palearctic*" and "*Cotinga*"; and would doubtless dwell on minor errors—"owlet" is defined as a "young owl", but it is also used for four genera of small strigids, and Canadians may be a little mortified to see the Christmas Bird Count described as "an annual bird count in USA"; last year, notwithstanding temperatures of minus 40° in some locations, there were 371 Christmas counts in Canada, per capita (a term which is defined in this dictionary) twice as many as were conducted by our more delicate cousins to the south!

"The Ornithologist's Dictionary" is a thoroughly workmanlike and useful publication. It will not become preferred bedtime reading, but as a daily tool it deserves a place on the desk of any serious ornithologist, whether professional or amateur.—DAVID BREWER, RR 1, Puslinch, ON N0B 2J0, Canada; e-mail: mbrewer@albedo.net

HANDBOOK OF BIRDS OF THE WORLD, VOLUME 12. PICATHARTES TO TITS AND CHICKADEES. Edited by Josep del Hoyo, Andrew Elliott, and David Christie. Lynx Edicions, Barcelona, Spain. 2007: 815 pp., 56 color plates, numerous color photographs and range maps. ISBN: 8496553426. $265 (cloth).—This large format (24 × 31 cm; 4.6 kg) 12th volume in this remarkable series begins with an essay entitled *Fossil Birds* by Kevin Caley. It is 45 pages in length, has a Glossary, the References section con-

tains 335 citations, and the essay is an excellent summary of what we know (and perhaps more importantly, what we do not know) about fossil birds. Included is a discussion of the evolution of birds (including the "tree-down" "ground-up" controversy) and the author concludes: ". . . [the] general opinion is that the evidence for birds being descendents of theropod dinosaurs is overwhelming." The text is supplemented by line-drawings by the author.

The bulk of the text consists of family and species accounts of the Picathartidae (Pithacartes), Timaliidae (babblers), Paradoxornithidae (parrotbills), Pomatostomidae (Australasian babblers), Orthonychidae (logrunners), Eupetidae (jewel-babblers and allies), Pachycephalidae (whistlers), Petroicidae (Australasian robins), Maluridae (fairy-wrens), Dasyornithidae (bristlebirds), Acanthizidae (thornbills), Epthianuridae (Australian chats), Neosittidae (sittellas), Climacteridae (Australasian treecreepers), and Paridae (tits and chickadees). The family accounts are extensive, often exceeding the length of the combined species accounts, and are lavishly illustrated with stunning color photographs. The family accounts vary in length, with the longest, the Timaliidae (with 309 species), occupying 64 pages including 95 photographs (some full-page), and several accounts (e.g., the Orthonychidae) with eight pages and less than a dozen photographs. The family accounts typically begin with a summary box that details Class, Order, Suborder and Family, a small map with world distribution in red, and a brief description of the characteristics of the family, habitat, number of genera, species, and subspecies, and conservation status. The sections of each family accounts generally are: Systematics, Morphological Aspects, Habitat, General Habits, Voice, Food and Feeding, Breeding, Movements, Relationship with Man, and Status and Conservation. There are no in-text references, but a General Bibliography at the end of each family account gives abbreviated references (corresponding full citations are in the References at the end of the book). The family accounts have a wealth of information including such things as debate over vernacular names. For example, in the Acantizidae account, the shift (which I have long opposed) from the traditional "Warbler" to "Gerygone" (the genus name) of a group of acanthizides is explained and the meaning of "Gerygone" given: "born of sound" or "born of song."

The species accounts (623 in this volume) typically begin with the common name, followed by the scientific name, the common name in French, German, and Spanish, other common names, and sections on Taxonomy, Distribution, Descriptive Notes (that include voice), Habitat, Food and Feeding, Breeding, Movements, and Status and Conservation. The account concludes with a bibliography with shortened citations as in the family accounts. The accounts of species I have worked with and know best (e.g., Tasmanian Scrubwren [*Sericornis humilis*], Slender-billed Thornbill [*Acanthiza iredalei*], Scrubtit [*Acanthornis magna*], Rufous Treecreeper [*Climacterus rufus*]) were excellent with accurate and pertinent information and citing the major references. Each species account includes a range map in up to three colors: yellow for breeding distribution, blue for non-breeding, and green for year-round.

The 56 color plates by Norman Arlott, Hilary Burn, John Cox, Ren Hathway, Ian Lewington, Chris Rose, Jan Wilczur, and Tim Worfolk, which accompany the species accounts, are uniformly excellent. As in previous volumes, the plates are on even-numbered pages and many have text or photographs printed on the previous page (back-side of the sheet). Thus, there is a faint image of print lines showing through onto the plate, but I found this not to be a distraction. The plates are interspersed in the corresponding text so the image is not more than a few pages from the text. Where appropriate, subspecies are illustrated as well as females of dimorphic species. For example, in the Varied Sittella (*Daphoenositta chrysoptera*), all five Australian subspecies are illustrated and two of five have female as well as male images; two of five New Guinea subspecies are illustrated, one with a female image. The References section is divided into References of Scientific Descriptions (1,020 entries) and General List of References (>3,000 full-citation entries). Both are gold mines of information. The index has individual species double-entered, for example: Varied Sittella and Sittella, Varied—a user-friendly feature.

This volume—and the entire series—represent a remarkably bold initiative. To produce comprehensive accounts of all families of birds and their nearly 10,000 species is a project of enormous proportions. That Lynx Edicions and their editorial staff have been able to bring together a product of such high quality is remarkable. The necessarily high price may limit the number of individuals who acquire the series, but every library ought to have one.—WILLIAM E. DAVIS JR., Professor Emeritus, Boston University, 23 Knollwood Drive, East Falmouth, MA 02536, USA; e-mail: wedavis@bu.edu

FALCONRY AND HUNTING IN ARABIA. By Faris Al-Timimi. Hancock House Publishers, Blaine, Washington, USA. 2007: 320 pages, 442 photographs. ISBN 978-0-97388-530-9. $120.00 (cloth).—Al-Timimi became a veterinarian at the University of Baghdad and for many years operated a clinic for trained falcons in Qatar, and more recently in Saudi Arabia. His purpose, as a non-falconer, is to reveal traditional attitudes and customs of Arab falconers, and the nature of their hunting falcons and their quarry. The narrative often rambles, and topics are only loosely assorted by chapter, and sometimes not at all by paragraph. This unusual style might be excused because English is not the author's primary language.

Chapters include a historical account of hunting in Arabia (but with few dates), the character of Arab hunters (really a description of how they go about falconry), an exhaustive description of their falcons (mainly Saker [*Falco cherrug*] and Peregrine [*F. peregrinus*] falcons), and a graphically illustrated chapter on diseases (often worse-case examples) of captive falcons. Plastic "astroturf", of the type commonly used as doormats, was introduced to Arabia (in Dubai) as a covering on falcon perches. It greatly reduced the incidence of disastrous infections on the bottom of the feet, not so much because it allows air flow under the feet, as the author asserts, but because the many plastic fingers cushion the feet and distribute the weight of the sedentary falcon more evenly, reducing pressure on prominent areas, and enhancing vascular circulation.

Another interesting but seemingly unrelated chapter describes Arab expeditions to Somalia in 1982 and Sudan in 1983. The main purpose of the latter was apparently to obtain antelope such as oryx (*Oryx* spp.), addax (*Addax nasomaculatus*), and gazelle (*Gazella* spp.) for private zoos in Qatar. The expeditions are illustrated by 44 color photos, most of which are of antelope. There is a chapter on taming and initial training of falcons. In pattern, these methods are not unlike those used in the West, except for the miserable practice of using a single suture, through both lower eyelids, passed over the top of head and tied to hold them up, preventing the falcon from seeing its new surroundings. Western falconers use a hood (probably introduced to the West by Arabs in the Crusades) extensively in the first days of training to achieve the same purpose without risk of tearing and scarring the eyelids.

Arab falconry involves only falcons; hawks are rarely used. Sakers are preferred to chase Houbara Bustards (*Chlamydotis undulata*) in direct flight from the falconer's glove. Female Peregrines are used less frequently but have become more popular. First-year migrant falcons are more prevalent, but adults (haggards) of both species are trapped and trained. Peregrines are apparently more fragile than Sakers and their monetary value plummets at the end of the hunting season because they do not hold up well through the long molt (Mar–Oct). Sakers are more durable in what the author calls "harsh" treatment by Arab falconers. Outstanding hunters are retained from season to season. Unwanted falcons are sold at greatly reduced rates or set free, the latter to uncertain fates.

In Arab falconry there is great emphasis on the appearance of each falcon, especially Sakers. As in the similar Gyrfalcon (*Falco rusticolus*), Sakers have immense plumage variation. Pale individuals are highly prized, dark birds a bit less so, and lastly there are the average individuals. The author maintains that plumage color and pattern are unrelated to performance, contrary to the widely held superstitions of Arab falconers. There are more than 178 color photographs of captive falcons in the chapter "The Arabs and Their Hunting Falcons", many of them full-page. Some of the birds are hooded. Included are photos of a few dozen Gyrfalcon and Saker study skins

held by the British Museum. The assumption is that Saker color and pattern variants come from different regions and are different "forms". Unfortunately, the living birds and most of the skins were from wintering areas and could not reveal regional patterns in nesting areas.

The author, Al-Timimi, maintains that falconry in Arabia is now the "sport" of a large proportion of the population, commoner and royalty alike. Falconry was certainly practiced among the nomads (Bedouin) and, after WW II, grew in favor among the royal families whose wealth created huge collections of trained falcons and their caretakers. In the last two decades, no doubt several thousands of falcons were in captivity in the Gulf Region in any year. Because of high turnover in the captive population, a few thousand wild Saker and Peregrine falcons were supplied by dealers each year to replace the losses. Dealers in Pakistan, Syria, Iraq, and Iran smuggled falcons to the Arabian Peninsula, sometimes with poor results for the birds. Dealers have expanded their quest for falcons across the whole of Central Asia, east to China where Sakers are numerous. The author does not cover up the conservation concerns, but he provides only his impressions, and few data.

Overall, the situation is changing. Captive-bred Gyrfalcons and gyr-hybrids with Peregrine and Saker falcons have grown greatly in popularity, not so much because of increased effectiveness in hunting, but because many are phenomenally handsome, especially in the eyes of sheikhs who pay great prices just to have them in their collection. These captive-bred falcons are imported legally from the West by the hundreds annually. But at the same time, many of those who can afford the costs have become distracted by involvement in their exploding economies. Falconry appears to be on the decline among the entitled families.

And then there are the "poor Houbara". They now migrate into the Peninsula so rarely that a sheikh may pay a huge reward for information on the whereabouts of one to hunt. Further, as photos in the book show, Pakastani trappers net hundreds, intending to smuggle them to the Peninsula where they are used as live lures to train falcons. Apparently, many die in transit. Houbara populations have crashed, and there are few alternate species the Arabs wish to hunt. Arabs have been forced to mount, at great cost, large hunting expeditions for Houbara to regions from Libya to Pakistan.

This book will not likely serve as a reference, but it provides considerable insight into the way falconry works in Arabia. These workings are markedly different from those in the West. Many North American falconers do not use falcons, but use hawks instead. On reading this account, falconers in the West who actually hunt with their birds, will come to more deeply appreciate their situation. As a life-long falconer, I am happy for the variety of raptors Western falconers use, the abundances of quarry that match the raptors and the abilities of falconers, the commitments of the falconers to perfection of the art, the fine veterinary care available, and the many regulations that effectively govern uses of our raptor and prey resources. I thank J. D. Remple for comments on this review.—JAMES H. ENDERSON, Professor Emeritus, Colorado College, 3215 Austin Drive, Colorado Springs, CO 80909, USA; e-mail: jenderson@coloradocollege.edu

SWAN. By Peter Young. Reaktion Books, Ltd., London, UK. 2008: 200 pages, 45 black and white plates, and 55 color plates, ISBN 978-1-86189349-9. $19.95 (paper).—This book is part of a series entitled ANIMAL edited by Jonathan Burt. Although the book includes biological and conservation information, there are many more pages dedicated to the documentation of the influence of swans on and interactions with humans.

The first chapter, "Clamorous Wings", includes a brief review of swan biology and natural history. Although mostly accurate, the biological treatment is superficial. It is stated in one place that eight species survive, but notes that ornithologists disagree on seven or nine species. No attempt is made to specify the "species" to which the disagreements refer.

Chapter 2, "Grace and Favour" is based on human observations of swans and begins with some of the early taxonomic works with some emphasis on illustrations of swans that accompanied the texts. Much of this chapter dis-

cusses swans in literature and art, as well as human impressions of swans.

Swan transformations (Chapter 3) are the stuff of fairy tales (The Ugly Duckling), mythology, and legend. Swan transformations appear in numerous cultures on almost every continent. Most are familiar with Leda and the Swan from Greek mythology where Zeus, in the form of a swan, seduces Leda. This story has been the subject of many works of art and is referred to in all kinds of literary works from poetry to novels. Numerous other swan/human transformations are discussed.

History (Chapter 4) discusses chronological representations of swans including using swans in place names, architecture, reference to objects, and influence on historical or scientific discoveries. For example, the "swan-necked" flask was used by Louis Pasteur to demonstrate that germs exist in the atmosphere. In 1727, Thomas Young observed the intersecting ripples set up by swans in a pond in Cambridge. He believed that light traveled in waves and interacted much the same as the waves generated by swans on the surface of the water. Young subsequently demonstrated interference patterns through light experiments supporting this wave theory of light.

Chapter 5 (Hazards) could have combined with conservation, as it concerns a combination of exploitation of swans by humans, and injuries and deaths caused by human related products or activities. Included in the discussion are shooting by vandals, the hazards of fish hooks, fishing line, oil and chemical spills, lead poisoning by ingestion of shotgun pellets and fishing sinkers, and collisions with structures such as power lines, wind turbines, and communications towers. This chapter also discusses uses of swans and swan parts from the 1770s to the early 1990s that are strongly implicated in the decimation of some species like the Trumpeter Swan (*Cygnus buccinator*). Swan feathers made the best quill pens, down was used to stuff pillows and mattresses, and flight feathers were used for hats, fans, and muffs. The Hudson's Bay Company shipped over 17,000 swan skins from Canada between 1853 and 1877. Also, discussed in this chapter are the traditional and cultural uses of swan feathers or parts by aboriginal or tribal groups for food, healing, and religious purposes or for practical applications like tying fishing flies.

Swans have been used for food (Chapter 6) for thousands of years. In the Old Testament, swans are classified as "unclean" along with other animals with dark meat. Included in this chapter are instructions for raising, preparing, cooking, and serving swans. In England, swans were often prepared for banquets and Christmas dinners until the arrival of the turkey from the New World in the sixteenth century.

Chapter 7 discusses swan conservation. The earliest legal protection of swans appears to have occurred in England. There is evidence that some Mute Swans (*Cygnus olor*) were owned in England prior to the year 1000 and that they had developed a way of marking them. Mute Swans had royal protection under a 1483 act of King Edward IV. The Crown's right over swans continues to this day under the *Wild Creatures and Forest Laws Act of 1971*. Protection in Canada and the United States began with the signing of the Migratory Bird Treaty in 1916. The author makes no mention of the subsequent treaties between the U.S. and Mexico, Japan, and the Soviet Union. This chapter discusses refuges and reserves established for swan protection in various countries, such as Red Rock Lakes National Wildlife Refuge in the U.S. One important reserve not mentioned, is the Xinjiang Bayinbuluke Swan Lake Nature Reserve in China. The recent controversy in the U.S. over Mute Swan control is mentioned in this chapter. A court ruled that Mute Swans, a species introduced by man into North America, were protected under the Migratory Bird Treaty. The author does not report on a recent federal law that removed introduced migratory bird species from federal protection. He also characterized the court decision as "In the end the hunters lost". It was never really a hunting issue.

The final chapter (Promotion) concerns the use of swans in promoting businesses, products, and organizations. Because of their positive image of elegance and grace, swans imply quality. It is not surprising that swans are used as a logo for advertising.

For some reason, the author omitted reference to Banko's classic monograph, *The Trumpeter Swan* (1960, North American Fauna, Number 63). Also missing is A. Lindsey Price's *Swans of the World, in Nature, His-*

tory, Myth and Art (1995, Council Oak Books). A reader looking for a biological summary of swans of the world will be disappointed. If, however, one is interested in the influence on and interaction with human civilization, you will enjoy this interesting little book.—JOHN E. CORNELY, The Trumpeter Swan Society, 3 Cliffrose, Littleton, CO 80127, USA; e-mail: johncornely@msn.com

BIRDS: THE ART OF ORNITHOLOGY. By Jonathan Elphick. Rizzoli International Publications Inc., 300 Park Avenue South, New York, USA. 2008: 336 pages and 300 illustrations. ISBN: 978-0-8478-3134-0. $19.95 (hardcover).—This volume is indeed broad in scope. It spans the millennia of bird art from Paleolithic cave wall paintings in southern France and northern Spain, and images left as frescos in Egyptian tombs through the present generation of bird painters. It is a formidable undertaking, and the author is to be commended for completing an admirable task. Text and illustrations trace the chronological development of this genre from early, stylized depictions to the more naturalistic images of the late 19th and 20th centuries.

As the author alludes to in the preface, with a volume of such broad scope, the most difficult task certainly would be who to include and who to exclude. In the end, any volume tracing the development of an art form depends on the desire of the author to include artists who seem to have made a significant contribution to the evolution of the subject matter. I feel Mr. Elphick has made a sensible selection of bird painters both past and present.

The first impression one receives upon perusing the volume is its rather small size, 140 × 160 mm (5½ by 6¼ in.). Apparently, dimensions of the original, much larger edition were reduced to make the publication more affordable. This is a laudable decision; however, the smaller format might be difficult for some to read. The illustrations are excellent in quality and are not overly affected by the reduced size.

Many of the artists discussed, some at length, are represented with reproductions of their work; others are not. For example, Bodani's painting *Two Icelandic Falcons*, vividly described by the author, is not shown. In a visual world we are too often left with the written word, and word descriptions can not take the place of the painted image. Understandably, the practical nature of a volume of this breadth limits the number of illustrations that can be included.

The artist's approach to bird illustration versus the painting of the subject will be debated for a long while. Suffice it to say there is a difference. Generally speaking, illustrations are more documentary in nature and do not attempt to exploit the medium to the same extent as paintings. It might have been interesting to show a reproduction of a Liljefors' oil or Carel Fabritius' image of the European Goldfinch (*Carduelis carduelis*) as examples of the more painterly qualities of bird art.

The scope and visual imagery of this volume remind readers that bird art has reflected world cultures since prehistoric times. Those who appreciate the beauty as well as the identity of birds will want to add *Birds: The Art of Ornithology* to their library.—DON RADOVICH, Professor Emeritus, Western State College of Colorado, 17232 Woodgate Road, Montrose, CO 81403, USA; e-mail: canyon.creek@earthlink.net

THE WILSON JOURNAL OF ORNITHOLOGY

Editor CLAIT E. BRAUN
5572 North Ventana Vista Road
Tucson, AZ 85750-7204
E-mail: TWILSONJO@comcast.net

Editorial Assistant NANCY J. K. BRAUN

Editorial Board RICHARD C. BANKS
KATHY G. BEAL
JACK CLINTON EITNIEAR
SARA J. OYLER-McCANCE

Review Editor MARY GUSTAFSON
Texas Parks and Wildlife Department
2800 South Bentsen Palm Drive
Mission, TX 78572, USA
E-mail: WilsonBookReview@aolcom

GUIDELINES FOR AUTHORS

Please consult the detailed "Guidelines for Authors" found on the Wilson Ornithological Society web site (http://www.wilsonsociety.org). All manuscript submissions and revisions should be sent to Clait E. Braun, Editor, *The Wilson Journal of Ornithology*, 5572 North Ventana Vista Road, Tucson, AZ 85750-7204, USA. *The Wilson Journal of Ornithology* office and fax telephone number are (520) 529-0365. The e-mail address is TWilsonJO@comcast.net.

NOTICE OF CHANGE OF ADDRESS

Notify the Society immediately if your address changes. Send your complete new address to Ornithological Societies of North America, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

The permanent mailing address of the Wilson Ornithological Society is: %The Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109. Persons having business with any of the officers may address them at their various addresses given on the inside of the front cover, and all matters pertaining to the journal should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Timothy J. O'Connell, Department of Natural Resource Ecology and Management, Oklahoma State University, 205 Life Sciences West, Stillwater, OK 74078; e-mail: oconnet@okstate.edu

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution. The fund will be administered by the Library Committee. Robert Payne, University of Michigan, is Chairman of the Committee. The Library currently receives over 200 periodicals as gifts and in exchange for *The Wilson Journal of Ornithology*. For information on the Library and our holdings, see the Society's web page at http://www.wilsonsociety.org. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: Josselyn Van Tyne Memorial Library, Museum of Zoology, The University of Michigan, 1109 Geddes Avenue, Ann Arbor, MI 48109-1079, USA. Contributions to the New Book Fund should be sent to the Treasurer.

This issue of *The Wilson Journal of Ornithology* was published on 5 September 2008.

Continued from outside back cover

582 Nest habitat selection of White-winged Scoters on Yukon Flats, Alaska
David E. Safine and Mark S. Lindberg

Short Communications

594 Use of legs and feet for control by scoters during aerial courtship
William J. Wilson

599 Bill entanglement in subcutaneously-anchored radio transmitters on Harlequin Ducks
Jeanine Bond and Daniel Esler

603 Estimate of *Trichomonas gallinae*-induced mortality in Band-tailed Pigeons, upper Carmel Valley, California, winter 2006-2007
Mark R. Stromberg, Walter D. Koenig, Eric L. Walters, and John Schweisinger

606 Winter ecology of Yellow Rails based on South Carolina specimens
William Post

610 Nest raising by Red-crowned Cranes in response to human-mediated flooding at Zhalong Nature Reserve, China
Qiang Wang and Feng Li

613 White-winged Diuca Finch (*Diuca speculifera*) nesting on Quelccaya Ice Cap, Perú
Douglas R. Hardy and Spencer P. Hardy

618 Nest success and nest predation of the endangered Rota White-eye (*Zosterops rotensis*)
Lainie Berry and Estanislao Taisacan

620 Predators at nests of the Western Slaty Antshrike (*Thamnophilus atrinucha*)
Corey E. Tarwater

625 Evidence for Bachman's Sparrow raising Brown-headed Cowbirds to fledging
Matthew J. Reetz, Elizabeth Farley, and Thomas A. Contreras

628 Simultaneous incubation by two females and nestling provisioning by four adults at a Savannah Sparrow nest
Nathan J. Zalik and Noah G. Perlut

631 Grey Heron (*Ardea cinerea*) predation on the Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus*)
Pierre A. Pistorius

633 Purple Swamphens (*Porphyrio porphyrio*) attempting to prey upon Black Swan (*Cygnus atratus*) eggs and preying upon a cygnet on an urban lake in Melbourne, Australia
Shandiya Balasubramaniam and Patrick-Jean Guay

635 Northern Fulmar predation of Common Murre
Stephan Lorenz and Sampath Seneveratne

637 Diet of nestling Black-crowned Night-herons in a mixed species colony: implications for Tern conservation
C. Scott Hall and Stephen W. Kress

641 Diet of the Long-eared Owl in the northern and central Negev Desert, Israel
Zohar Leader, Yoram Yom-Tov, and Uzi Motro

645 First observed instance of polygyny in Flammulated Owls
Brian D. Linkhart, Erin M. Evers, Julie D. Megler, Eric C. Palm, Catherine M. Salipante, and Scott W. Yanco

648 The Giant Hummingbird (*Patagona gigas*) in the mountains of central Argentina and a climatic envelope model for its distribution
Henrik von Wehrden

651 Giant Hummingbirds (*Patagona gigas*) ingest calcium-rich minerals
Cristián F. Estades, M. Angélica Vukasovic, and Jorge A. Tomasevic

654 Nocturnal foraging observations of the Blue-crowned Motmot (*Momotus momota*) in San José, Costa Rica
Alejandro Solano-Ugalde and Agustina Arcos-Torres

655 Kleptoparasitism by Grey Kingbirds (*Tyrannus dominicensis*) in Barbados
Sarah E. Overington, Laure Cauchard, and Kimberly-Ann Côté

657 Double-scratching by Yellow-headed Blackbirds
Alan de Queiroz

660 **Ornithological Literature**
Compiled by Mary Gustafson and Clait E. Braun

The Wilson Journal of Ornithology

(formerly *The Wilson Bulletin*)

Volume 120, Number 3 CONTENTS September 2008

Major Articles

433 Genetic structure of breeding and wintering populations of Swainson's Warbler
Kevin Winker and Gary R. Graves

446 Does age influence territory size, habitat selection, and reproductive success of male Canada Warblers in central New Hampshire?
Leonard R. Reitsma, Michael T. Hallworth, and Phred M. Benham

455 Solitary winter roosting of Ovenbirds in core foraging area
David R. Brown and Thomas W. Sherry

460 Reproductive success of the Puerto Rican Vireo in a montane habitat
Adrianne G. Tossas

467 Nest defense by Carolina Wrens
Kelly A. D'Orazio and Diane L. H. Neudorf

473 Nests, eggs, and parental care of the Puna Tapaculo (*Scytalopus simonsi*)
Peter A. Hosner and Noemí E. Huanca

478 Phylogeographic patterns of differentiation in the Acorn Woodpecker
Magali Honey-Escandón, Blanca E. Hernández-Baños, Adolfo G. Navarro-Sigüenza, Hesiquio Benítez-Díaz, and A. Townsend Peterson

494 Diet of Acorn Woodpeckers at La Primavera Forest, Jalisco, Mexico
Veronica Carolina Rosas-Espinoza, Elisa Maya-Elizarraras, Oscar Francisco Reyna Bustos, and Francisco Martin Huerta-Martinez

499 Seasonal variation in acoustic signals of Pileated Woodpeckers
Sarah B. Tremain, Kyle A. Swiston, and Daniel J. Mennill

505 Common Poorwill activity and calling behavior in relation to moonlight and predation
Christopher P. Woods and R. Mark Brigham

513 Maximizing detection probability of wetland-dependent birds during point-count surveys in northwestern Florida
Christopher P. Nadeau, Courtney J. Conway, Bradley S. Smith, and Thomas E. Lewis

519 Male song variation of Green Violetear (*Colibri thalassinus*) in the Talamanca Mountain Range, Costa Rica
Gilbert Barrantes, César Sánchez, Branko Hilje, and Rodolfo Jaffé

525 Metabolizable energy in Chinese Tallow fruit for Yellow-rumped Warblers, Northern Cardinals, and American Robins
Michael J. Baldwin, Wylie C. Barrow Jr., Clinton Jeske, and Frank C. Rohwer

531 Foraging ecology of High Andean insectivorous birds in remnant *Polylepis* forest patches
Huw Lloyd

545 Nesting biology of the Giant Conebill (*Oreomanes fraseri*) in the High Andes of Bolivia
J. R. A. Cahill, E. Matthysen, and N. E. Huanca

550 Bird density and mortality at windows
Stephen B. Hagar, Heidi Trudell, Kelly J. McKay, Stephanie M. Crandall, and Lance Mayer

565 Ectoparasites affect hemoglobin and percentages of immature erythrocytes but not hematocrit in nestling Eastern Bluebirds
Reneé E. Carleton

569 Observations on flocking behavior of Worthen's Sparrow (*Spizella wortheni*) and occurrence in mixed-species flocks
Julio C. Canales-Delgadillo, Laura M. Scott-Morales, Mauricio Cotera Correa, and Marisela Pando Moreno

575 Status of Crested Penguin (*Eudyptes* spp.) populations on three islands in southern Chile
David A. Oehler, Steve Pelikan, W. Roger Fry, Leonard Weakley Jr., Alejandro Kusch, and Manuel Marin

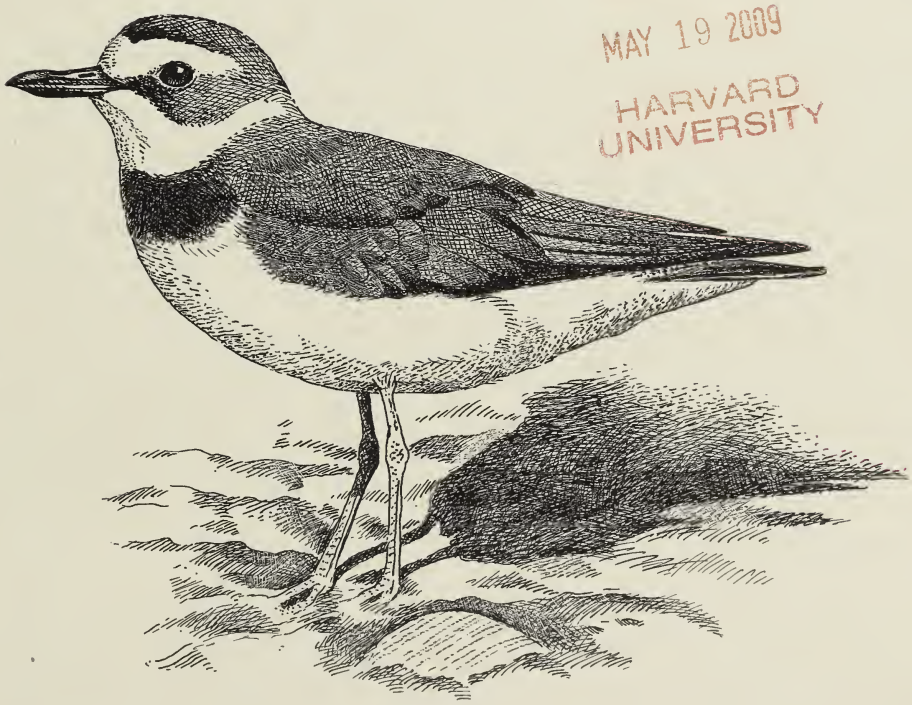
Continued on inside back cover

8424
.16

The Wilson Journal of Ornithology

Volume 120, Number 4, December 2008

MCZ
LIBRARY
MAY 19 2009
HARVARD
UNIVERSITY



Published by the
Wilson Ornithological Society

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED 3 DECEMBER 1888

Named after ALEXANDER WILSON, the first American ornithologist.

President—James D. Rising, Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada; e-mail: rising@zoo.utoronto.ca

First Vice-President—E. Dale Kennedy, Biology Department, Albion College, Albion, MI 49224, USA; e-mail: dkennedy@albion.edu

Second Vice-President—Robert C. Beason, USDA, Wildlife Services, 6100 Columbus Avenue, Sandusky, OH 44870, USA; e-mail: beason@netzero.com

Editor—Clait E. Braun, 5572 North Ventana Vista Road, Tucson, AZ 85750, USA; e-mail: TWILSONJO@comcast.net

Secretary—John A. Smallwood, Department of Biology and Molecular Biology, Montclair State University, Montclair, NJ 07043, USA; e-mail: smallwoodj@montclair.edu

Treasurer—Melinda M. Clark, 52684 Highland Drive, South Bend, IN 46635, USA; e-mail: MClark@tcservices.biz

Elected Council Members—Carla J. Dove, Greg H. Farley, Daniel Klemm Jr., and Mia R. Revels (terms expire 2009); Robert S. Mulvihill, and Timothy O'Connell (terms expire 2010); Jameson F. Chace, Sara R. Morris, and Margaret A. Voss (terms expire 2011).

Membership dues per calendar year are: Active, $21.00; Student, $15.00; Family, $25.00; Sustaining, $30.00; Life memberships, $1,000.00 (payable in four installments).

The Wilson Journal of Ornithology is sent to all members not in arrears for dues.

THE WILSON JOURNAL OF ORNITHOLOGY

(formerly *The Wilson Bulletin*)

THE WILSON JOURNAL OF ORNITHOLOGY (ISSN 1559-4491) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

All articles and communications for publications should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, MI 48109, USA.

Subscriptions, changes of address, and claims for undelivered copies should be sent to OSNA, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710, USA. Phone: (254) 399-9636; e-mail: business@osnabirds.org. Back issues or single copies are available for $12.00 each. Most back issues of the journal are available and may be ordered from OSNA. Special prices will be quoted for quantity orders. All issues of the journal published before 2000 are accessible on a free web site at the University of New Mexico library (http://elibrary.unm.edu/sora/). The site is fully searchable, and full-text reproductions of all papers (including illustrations) are available as either PDF or DjVu files.

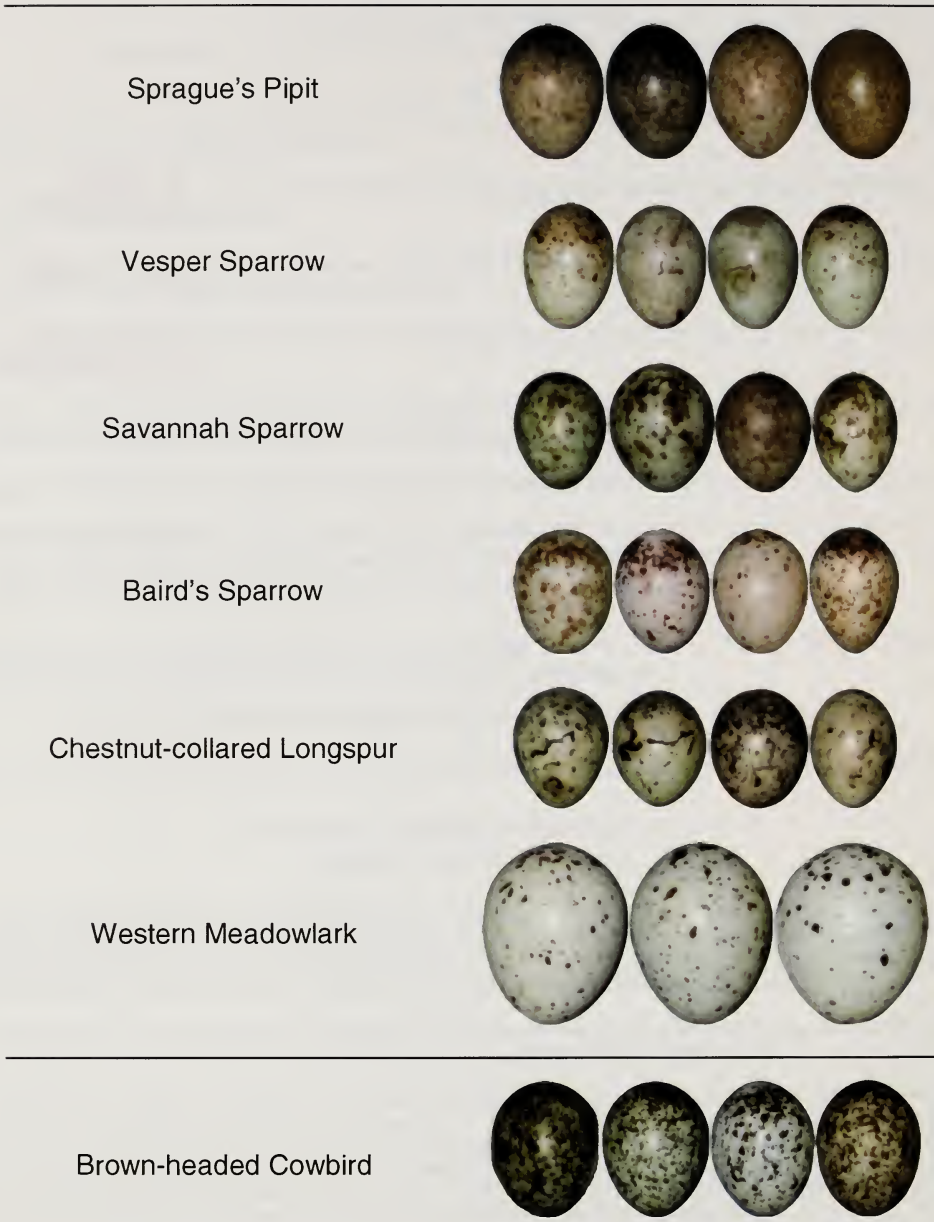
© Copyright 2008 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, KS 66044, U.S.A.

COVER: Wilson's Plover (*Charadrius wilsonia*). Illustration by Don Radovich.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

MCZ
LIBRARY
MAY 19 2009
HARVARD
UNIVERSITY



FRONTISPIECE. Examples of eggs of Brown-headed Cowbird (*Molothrus ater*) and six common grassland passerines in south-central Saskatchewan. Top row to second row from the bottom are host species: Sprague's Pipit (*Anthus spragueii*), Vesper Sparrow (*Pooecetes gramineus*), Savannah Sparrow (*Passerculus sandwichensis*), Baird's Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). Bottom row: parasitic Brown-headed Cowbird. Experimentally parasitizing nests of these species with cowbird-like eggs and non-mimetic (blue) eggs, Klippenstine and Sealy (pages 667–673) recorded more blue eggs ejected than cowbird eggs by each species, which suggests similarity in appearance of cowbird and host eggs impeded discrimination and may represent a form of cowbird egg mimicry.

The Wilson Journal *of Ornithology*

Published by the Wilson Ornithological Society

VOL. 120, NO. 4 December 2008 PAGES 667–962

The Wilson Journal of Ornithology 120(4):667–673, 2008

DIFFERENTIAL EJECTION OF COWBIRD EGGS AND NON-MIMETIC EGGS BY GRASSLAND PASSERINES

DWIGHT R. KLIPPENSTINE[1,2] AND SPENCER G. SEALY[1,3]

ABSTRACT.—Grassland passerines are purported to tolerate parasitism by Brown-headed Cowbirds (*Molothrus ater*) because of adaptations by cowbirds that constrain egg discrimination and removal by their hosts, i.e., evolutionary equilibrium, rather than because of an absence of these defensive behaviors, i.e., evolutionary lag. We tested these hypotheses by experimentally parasitizing six grassland species with cowbird-like eggs and non-mimetic (blue) eggs in south-central Saskatchewan. Sprague's Pipits (*Anthus spragueii*), Vesper (*Pooecetes gramineus*), Savannah (*Passerculus sandwichensis*), and Baird's (*Ammodramus bairdii*) sparrows, and Chestnut-collared Longspurs (*Calcarius ornatus*) accepted all or nearly all cowbird eggs, but ejected or attempted to eject between 9 and 20% of blue eggs with 54% of rejected eggs not removed from the nests, i.e., failed ejection attempts. Western Meadowlarks (*Sturnella neglecta*) ejected an intermediate number of cowbird eggs (67%) and most blue eggs (92%), none of which was recovered. Ejection of non-mimetic eggs versus cowbird eggs by each species suggests that similarity in appearance of cowbird eggs and hosts' eggs impeded discrimination and may represent a form of cowbird egg mimicry. The low number of blue eggs ejected by five of the six species, their failure to remove these eggs from the nest sites, and the damage wrought on some hosts' eggs during ejection suggest the morphology of cowbird eggs also constrains ejection behavior. These results support the evolutionary equilibrium hypothesis as the better explanation for acceptance of cowbird parasitism observed in these grassland passerines. *Received 4 May 2007. Accepted 15 February 2008.*

Hosts of the parasitic Brown-headed Cowbird (*Molothrus ater*) generally accept or reject cowbird eggs, depending on their ability to discriminate and eject foreign eggs from their nests (Rothstein 1975a, Peer and Sealy 2004). Birds learn the appearance of their own eggs as they are laid, which permits detection of foreign eggs that differ visually from the hosts' eggs (reviewed in Kilner 2006). Ejection is the removal of a targeted egg by grasping its girth, i.e., grasp-ejection, or puncturing the shell and lifting the egg out of the nest or removing it piecemeal, i.e., puncture-ejection (Underwood and Sealy 2006). Cowbird parasitism often reduces the reproductive success of hosts (Lorenzana and Sealy 1999); therefore, removal of cowbird eggs should benefit species that are parasitized frequently (Rothstein 1990, Underwood and Sealy 2002).

Hosts of the Brown-headed Cowbird (hereafter "cowbird") that inhabit the grasslands of

[1] Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada.

[2] Current address: 896 Garfield Street North, Winnipeg, MB R3G 2M7, Canada.

[3] Corresponding author; e-mail: sgsealy@cc.umanitoba.ca

the Great Plains have been presumed to possess egg discrimination and ejection behavior because they have nested in sympatry with cowbirds for thousands of years (Friedmann 1929, Mayfield 1965). Moreover, cowbird parasitism significantly reduces breeding success in parasitized grassland hosts (Hill 1976, Elliott 1978, Davis and Sealy 2000, Davis 2003). However, of the species regularly listed as grassland passerines in North America (Mengel 1970, Knopf 1994), only Eastern (*Sturnella magna*) and Western (*S. neglecta*) meadowlarks are known to regularly eject cowbird eggs (Peer et al. 2000). Instead, acceptance of experimentally added cowbird eggs by several grassland passerines (Hill and Sealy 1994, Sealy 1999, Peer et al. 2000, Davis et al. 2002) and observations of cowbirds fledging from naturally parasitized nests (Elliott 1978, Davis and Sealy 2000, Davis 2003) suggest that most grassland species tolerate parasitism.

Grassland passerines, according to the evolutionary lag hypothesis, may accept parasitic eggs because of insufficient selective pressure to evolve egg discrimination and ejection (Rothstein 1975a, 1990; Davies and Brooke 1989). Several studies have demonstrated that grassland passerines are infrequently parasitized compared with hosts that occupy adjacent habitats, although there is variability (Smith et al. 2000). Moreover, the selective pressure provided by parasitism is presumably higher today than in the past (Davis and Sealy 2000). This reflects recent increases in cowbirds and greater accessibility of grassland hosts that result from habitat fragmentation and creation of suitable perches (Davis and Sealy 2000). Evolutionary lag may also arise if the mutations governing egg discrimination and ejection have not developed or spread throughout the host's population (Rothstein 1990).

The evolutionary equilibrium hypothesis posits that even if egg ejection behavior has evolved, grassland passerines may accept cowbird eggs because ejection is too costly (Rohwer and Spaw 1988, Lotem and Nakamura 1998). Ejection may be costly when parasites have counter-evolved adaptations that cause hosts to make recognition errors, i.e., eject the wrong egg, or ejection errors, i.e., damage their own eggs during the ejection process (Davies et al. 1996, Lotem and Nakamura 1998). Several authors have suggested that a generalized form of "mimicry" exists between color and maculation of cowbird eggs and those of grassland passerines, which may hinder egg discrimination and lead to recognition errors (Peer et al. 2000, Davis et al. 2002, Klippenstine 2005). Cowbird eggs are also larger, rounder, and have thicker shells, which may impede egg ejection by intolerant hosts and result in ejection errors (Rohwer and Spaw 1988, Picman 1989). Evolutionary equilibrium is supported by experimental evidence showing that several grassland passerines are more likely to eject foreign eggs if they are non-mimetic and undersized (Peer et al. 2000, Davis et al. 2002).

Our goal was to examine which of these hypotheses better explains the apparent acceptance of cowbird parasitism by grassland hosts. We experimentally parasitized six grassland species (Sprague's Pipits [*Anthus spragueii*], Vesper Sparrows [*Pooecetes gramineus*], Savannah Sparrows [*Passerculus sandwichensis*], Baird's Sparrows [*Ammodramus bairdii*], Chestnut-collared Longspurs [*Calcarius ornatus*], and Western Meadowlarks) with real and model cowbird eggs and non-mimetic eggs to assess their (1) tolerance of parasitism, (2) ability to discriminate foreign eggs, and (3) ability to remove foreign eggs from their nests. If these passerines accept cowbird eggs because of evolutionary lag, we hypothesized that hosts would accept both cowbird and non-mimetic eggs (Table 1). If at equilibrium with cowbird parasitism, we hypothesized that differences would be recorded in frequency and success of ejection

TABLE 1. Possible outcomes of experimental parasitism on grassland passerines.

	Problems with . . .			
Egg type	Discrimination only	Removal only	Discrimination and removal	Neither
Cowbird	Accepted	Attempted ejection	Accepted	Ejected
Non-mimetic	Ejected	Attempted ejection	Attempted ejection	Ejected

with different egg treatments. If mimicry has evolved, non-mimetic eggs should be ejected more often than cowbird eggs, whereas difficulties in ejecting "cowbird-sized" eggs should result in more failed ejection attempts than successful ejections (Table 1).

METHODS

Fieldwork was conducted in south-central Saskatchewan, Canada, from 7 May to 1 July 2001 and 9 May to 15 July 2002. Sites were 60 km south of Regina and widely dispersed within a 100-km^2 area centered about the abandoned town of Dummer (49° 50′ N, 104° 49′ W). The 18 sites consisted of 7 privately owned pastures of mixed-grass prairie and 6 alfalfa (*Medicago sativa*), 1 fallow, 1 stubble, and 3 crested wheatgrass (*Agropyron cristatum*) fields that ranged from 0.5 to over 500 ha. Most nests were found with a "dragging rope" pulled over the ground to flush incubating adults (Davis et al. 2002), although some nests were found while inspecting other nests.

Each nest was experimentally parasitized with one of four egg treatments: real cowbird eggs, model cowbird eggs, real immaculate blue eggs, or model immaculate blue eggs (Fig. 1). Cowbird and blue eggs were used to assess host discrimination of foreign eggs because cowbird egg treatments were considered mimetic in appearance to the eggs of all six grassland passerine species studied (Baicich and Harrison 1997); the immaculate blue egg treatments were considered non-mimetic (Fig. 1, Frontispiece). We note that despite recent evidence for birds 'seeing' objects in the UV spectrum, no evidence exists to suggest that acceptance or rejection is related to UV reflectance (Underwood and Sealy 2008). We used model eggs as well as real eggs because no significant bias has been attributed to use of model eggs (Rothstein 1975a, Hill and Sealy 1994, Peer et al. 2000), and because they provided a means to assess the method of ejection used by grassland hosts. Preferential ejection of real eggs would signify puncture-ejection, as models cannot be pierced (Davis et al. 2002, Underwood and Sealy 2006). Conversely, the ejection of both model and real eggs would imply grasp ejection (Davis et al. 2002, Underwood and Sealy 2006).

Real cowbird eggs were collected from naturally parasitized nests of Red-winged Blackbirds (*Agelaius phoeniceus*) and Brewer's Blackbirds (*Euphagus cyanocephalus*) and stored at ~5° C for up to 5 days until they were used to test nests. Model eggs were made of plaster-of-Paris following Rothstein's (1970) protocol and were ($\bar{x}$ ± SE) 20.84 ± 0.04 mm × 16.97 ± 0.03 mm (n = 101), which approximated the dimensions of real cowbird eggs (21.45 × 16.42 mm, n = 127; Lowther 1993); however, they averaged slightly heavier (3.40 ± 0.03 g, n = 101 vs. 3.12 g, n = 181; Lowther 1993). Folkart® and Liquitex® acrylic paints were used to create the colors of the eggs. One part wicker white (#901 FA), one-quarter part medium gray (#425 FA), and one-quarter part burnt umber (#462 FA) were used in combination to simulate the off-white to slightly brown ground color of cowbird eggs. The reddish-brown maculation consisted of one part burnt umber and one part wicker white, whereas the gray maculation was composed of one part medium gray and one part wicker white; both were then spattered on the surface of the egg with a toothbrush to resemble a typical cowbird egg. The solid blue ground color was one part cerulean blue (#470 L) and one part light blue violet (#680 L). Painted eggs were waterproofed with a coat of lacquer, which also gave them a realistic shine.

Clutches during laying or in early incubation (days 0 through 7-8) received one of the four egg treatments. It should be noted that, because real cowbird eggs were not available throughout the entire experiment, more model

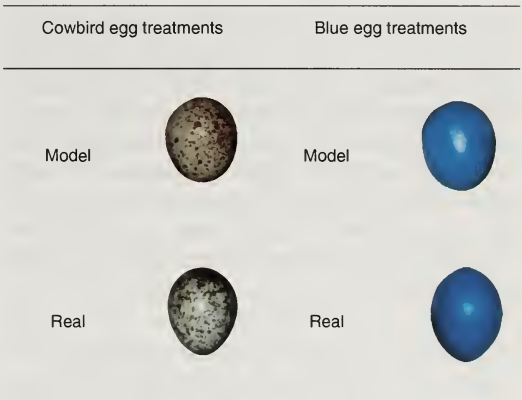


FIG. 1. Four egg treatments used to parasitize nests.

egg treatments were used than real egg treatments; but as much as possible, treatments were assigned randomly. Each nesting pair was tested only once and we assumed that unmarked females at nests tested in 2001 were not tested again in 2002. Experimental eggs were left in nests for 5 days and inspected on days 1, 2, 4, and 5. Eggs were considered accepted if they remained undamaged and tended in nests for 5 days, and rejected if they disappeared from an otherwise active nest (successful ejection) or were damaged, i.e., chipped or scratched, but remained in the active nest (attempted ejection). A 5-day test period was considered sufficient, as most rejections occur within 2 days and rarely after 5 days (Rothstein 1975b, Underwood and Sealy 2006). We removed accepted eggs following the 5-day test period and all nests, regardless of experimental outcome, were inspected until the host's eggs hatched or the nest failed. Ejected eggs found within 5 m of the nest rim were recorded, as were host eggs damaged or missing following ejection.

Models were cleaned after each experiment with a dilute alcohol solution and re-used; real cowbird eggs were used only once. All naturally parasitized nests also received experimental eggs, as ignoring nests already parasitized may exclude individuals prone to acceptance and bias the sample toward rejection. No host eggs were removed from nests tested.

Statistical Analyses.—The Log-Likelihood Ratio was used to compare the frequency of ejection between egg types within a species. This test was selected over the Fisher Exact Test because it performs well with expected values less than five (Zar 1996). All tests used *alpha* = 0.05. Sprague's Pipits received only model cowbird eggs and model blue eggs because the expected number of nests was small. The experimental egg at 16 nests was removed after 4 days due to errors in estimating the hatching date; however, these did not affect the overall results and were included in the final analyses. Nests that were deserted or depredated during the 5-day test period were excluded from analysis.

RESULTS

Natural cowbird parasitism was recorded for all six species and ranged from 5 to 28% with a pooled frequency of 15% for the entire community for both years (n = 306 nests): Sprague's Pipit (16%, n = 19 nests), Vesper Sparrow (20%, n = 40), Savannah Sparrow (28%, n = 47), Baird's Sparrow (16%, n = 70), Chestnut-collared Longspur (5%, n = 96), and Western Meadowlark (15%, n = 34). Of the 266 nests tested experimentally, 20% (n = 54) failed before a response could be measured, 4% (n = 10) were excluded because their fates could not be ascertained, and of the 76% (n = 202) of nests that were successful, 16% (n = 33) rejected and 84% (n =169) accepted the experimental egg.

Real versus Model Eggs.—No statistical tests were performed to investigate differences between model and real versions of either cowbird or blue eggs because so few rejections were recorded in most treatments (Table 2). More real blue eggs than model blue eggs appeared to be rejected (attempted and successful combined) by most species (Table 2). We presume this difference resulted from the inability of hosts to make discernible marks

TABLE 2. Frequency of rejection[a] (%) of experimentally added model and real cowbird and blue eggs (*significant difference at *alpha* = 0.05).

	% Frequency of rejection (n)						
	Cowbird egg treatments			Blue egg treatments			P value (cowbird vs. blue)
Species	Model	Real	Combined	Model	Real	Combined	
Sprague's Pipit	0.0 (8)		0.0 (8)	16.7 (6)		16.7 (6)	0.180
Vesper Sparrow	0.0 (11)	0.0 (4)	0.0 (15)	10.0 (1)	40.0 (5)	20.0 (15)	0.034*
Savannah Sparrow	11.1 (9)[b]	0.0 (5)	7.1 (14)	0.0 (8)	28.6 (7)	13.3 (15)	0.581
Baird's Sparrow	0.0 (20)	0.0 (6)	0.0 (26)	14.3 (14)	28.6 (7)	19.0 (21)	0.009*
Chestnut-collared Longspur	0.0 (17)	0.0 (9)	0.0 (26)	0.0 (21)	27.3 (11)	9.4 (32)	0.054
Western Meadowlark	70.0 (10)	50.0 (2)	66.7 (12)	90.9 (11)	100.0 (1)	91.7 (12)	0.121

[a] Includes both successful and failed ejection attempts.
[b] Ejection was suspected given the timing of the event.

on the models during failed ejection attempts rather than due to the method of ejection. The actual frequency of rejection for each species, therefore, may have been higher than reported (Table 2).

Cowbird versus Blue Eggs.—Sprague's Pipits, Vesper and Baird's sparrows, and Chestnut-collared Longspurs accepted all cowbird eggs (Table 2). Savannah Sparrows accepted all but one cowbird egg (Table 2), which disappeared between 4 and 5 days after "parasitism." This nest was later depredated and, given the timing of the event, we ascertained that a predator most likely removed the egg. Western Meadowlarks accepted 33% (n = 12) of the cowbird eggs and rejected the other eight within 48 hrs (Table 2).

Sprague's Pipits, Vesper, Savannah, and Baird's sparrows, and Chestnut-collared Longspurs rejected a small proportion of blue eggs (Table 2). Sprague's Pipits, Savannah Sparrows, and Chestnut-collared Longspurs rejected all blue eggs within 48 hrs, whereas Vesper Sparrows rejected one of three and Baird's Sparrows rejected one of four blue eggs between 2 and 5 days, and 2 and 3 days, respectively. Western Meadowlarks rejected 92% (n = 12) of the blue eggs within 48 hrs (Table 2).

Successful versus Failed Ejection Attempts.—Seven (54%) of the 13 rejected blue eggs reported for Sprague's Pipits, Vesper, Savannah, and Baird's sparrows, and Chestnut-collared Longspurs were classified as failed ejection attempts (Table 3). Of the six remaining ejections (46%) in which the blue egg was completely removed from the nest, two eggs were recovered within 5 m of the nest rims. Western Meadowlarks successfully ejected all egg treatments and none was recovered within 5 m of the nest rims.

Egg Loss.—One Savannah Sparrow egg disappeared after a blue egg had been ejected (0.50 eggs lost/blue egg ejected) and three Western Meadowlark eggs disappeared during two separate ejections of blue eggs (0.27 eggs lost/blue egg ejected); no other egg loss was noted among the four remaining species.

DISCUSSION

Our findings suggest the acceptance or partial acceptance of cowbird eggs by Sprague's Pipits, Vesper, Savannah, and Baird's sparrows, Chestnut-collared Longspurs, and Western Meadowlarks is best explained by the evolutionary equilibrium hypothesis. The ejection of foreign eggs reveals that all six species have evolved egg recognition and egg ejection in response to cowbird parasitism. Egg recognition is implied because birds do not simply remove discordant eggs (Rothstein 1975b, 1978) and the capacity to discriminate foreign eggs has little or no use outside the context of interspecific brood parasitism (Underwood and Sealy 2002, Kilner 2006). The preferential ejection of real blue eggs over model blue eggs by five of the six species suggests puncture ejection; however, only one recovered real blue egg showed signs of puncture, and this occurred after attempts over several days by the Savannah Sparrow pair to remove the egg. In contrast, ejection of solid plaster eggs by Western Meadowlarks, Sprague's Pipits, and Vesper Sparrows, and the recovery of an intact real blue egg ejected from a Chestnut-collared Longspur nest suggest grasp ejection. These findings do not support the evolutionary lag hypothesis, which states that hosts ac-

TABLE 3. Successful and failed ejections for both model and real blue eggs.

Species (n)	Number successful ejections		Number failed ejections	
	Model eggs	Real eggs	Model eggs	Real eggs
Sprague's Pipit (1)	1[a]		0	
Vesper Sparrow (3)	1	0	0	2
Savannah Sparrow (2)	0	1	0	1
Baird's Sparrow (4)	0	1	2	1
Chestnut-collared Longspur (3)	0	2[b]	0	1
Western Meadowlark (12)	10	1	0	0

[a] Egg was recovered 15 cm from the nest rim.
[b] One intact egg was found 20 cm from the nest rim; the other was not recovered.

cept parasitic eggs because they have not yet evolved egg discrimination and ejection (Rothstein 1975a, 1990; Davies and Brooke 1989).

More importantly we observed that the ability of all six grassland passerines to recognize and eject a foreign egg depended on the egg's parameters. Such plasticity is the hallmark of the evolutionary equilibrium hypothesis, which states that hosts accept or reject parasitic eggs based on the probability of making recognition and ejection errors (Rohwer and Spaw 1988, Lotem and Nakamura 1998). The differential ejection of blue eggs over cowbird eggs by all six species, for example, implies that hosts were hesitant to eject the latter, presumably because they are mimetic and are more likely to induce a recognition error. The high number of failed ejection attempts by five of the six species and the egg loss observed in Western Meadowlark and Savannah Sparrow nests following ejection of blue eggs implies that size and shape of cowbird eggs has evolved to impede grasp ejection by these hosts; although the influence of the thicker cowbird egg shell in preventing puncture ejection should be investigated further.

The evolutionary lag hypothesis only partially explains the pattern of ejection we observed. In particular, a mixture of acceptance and rejection could be observed in a population if egg discrimination and rejection have only recently evolved, and have begun to spread throughout the host's population (Peer et al. 2000). Western Meadowlarks examined in this study, for example, may consist of two-thirds rejecters and one-third accepters. The failed ejection attempts may reflect the recent development of a new skill. These ideas seem unlikely because we observed acceptance of naturally parasitized cowbird eggs by hosts that ejected an experimentally added cowbird egg or blue egg, which demonstrates that one host can be both tolerant and intolerant of foreign eggs. The spread of rejection behavior does not explain the differential ejection of non-mimetic eggs over cowbird eggs observed in this study or the preferential ejection of undersized eggs reported by Peer et al. (2000); presumably a truly mixed population of rejecters and accepters would reject all foreign eggs in roughly the same proportion. Our results suggest that grassland passerines tolerate parasitism because cowbirds have counter-evolved specific adaptations to the appearance and morphology of their eggs in response to the evolution of egg discrimination and ejection by host species.

ACKNOWLEDGMENTS

We are indebted to the landowners who permitted us to use their land. We thank M. A. Talbot and N. L. Haalboom for their hard work and Cornelius Klippenstine for use of his farmhouse. L. C. Graham, N. C. Kenkel, and M. D. Kujath commented on early drafts of the manuscript and offered their support throughout this project. D. E. Burhans and two anonymous reviewers provided constructive comments that improved the manuscript. This study was funded by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada to S. G. Sealy and through in-kind services provided by S. K. Davis and the Saskatchewan Watershed Authority (formerly Saskatchewan Wetlands Conservation Corporation).

LITERATURE CITED

Baicich, P. J. and C. J. O. Harrison. 1997. Nests, eggs, and nestlings of North American birds. Second Edition. Academic Press, New York, USA.

Davies, N. B. and M. de L. Brooke. 1989. An experimental study of co-evolution between the Cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. Journal of Animal Ecology 58:207–224.

Davies, N. B., M. de L. Brooke, and A. Kacelnik. 1996. Recognition errors and probability of parasitism determine whether Reed Warblers should accept or reject mimetic cuckoo eggs. Proceedings of the Royal Society of London, Series B 263: 925–931.

Davis, S. K. 2003. Nesting ecology of mixed-grass prairie songbirds in southern Saskatchewan. Wilson Bulletin 115:119–130.

Davis, S. K. and S. G. Sealy. 2000. Cowbird parasitism and nest predation in fragmented grasslands of southwestern Manitoba. Pages 220–228 *in* Ecology and management of cowbirds and their hosts: studies in the conservation of North American passerine birds (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Editors). University of Texas Press, Austin, USA.

Davis, S. K., D. R. Klippenstine, and R. M. Brigham. 2002. Does egg rejection account for the low incidence of cowbird parasitism in Chestnut-collared Longspurs (*Calcarius ornatus*)? Auk 119: 556–560.

Elliott, P. F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. Auk 95:161–167.

Friedmann, H. 1929. The cowbirds: a study in the biology of social parasitism. C. C. Thomas, Springfield, Illinois, USA.

Hill, D. P. and S. G. Sealy. 1994. Desertion of nests parasitized by cowbirds: have Clay-colored Sparrows evolved an anti-parasite defence? Animal Behaviour 48:1063–1070.

Hill, R. A. 1976. Host-parasite relationships of the Brown-headed Cowbird in a prairie habitat of west-central Kansas. Wilson Bulletin 88:555–565.

Kilner, R. M. 2006. The evolution of egg colour and patterning in birds. Biological Reviews 81:383–406.

Klippenstine, D. R. 2005. Can egg mimicry by Brown-headed Cowbirds explain the acceptance of brood parasitism by grassland passerines? Thesis. University of Manitoba, Winnipeg, Canada.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247–257.

Lorenzana, J. C. and S. G. Sealy. 1999. A meta-analysis of the impact of parasitism by the Brown-headed Cowbird on its hosts. Studies in Avian Biology 18:241–253.

Lotem, A. and H. Nakamura. 1998. Evolutionary equilibria in avian brood parasitism: an alternative to the "arms race-evolutionary lag" concept. Pages 223–235 *in* Parasitic birds and their hosts: studies in coevolution (S. I. Rothstein and S. K. Robinson, Editors). Oxford University Press, Oxford, United Kingdom.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). The birds of North America. Number 47.

Mayfield, H. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4:13–28.

Mengel, R. M. 1970. The North American Central Plains as an isolating agent in bird speciation. Pages 280–340 *in* Pleistocene and recent environments of the Central Great Plains (W. Dort and J. K. Jones, Editors). University of Kansas Press, Lawrence, USA.

Peer, B. D. and S. G. Sealy. 2004. Correlates of egg rejection in hosts of the Brown-headed Cowbird. Condor 106:580–599.

Peer, B. D., S. K. Robinson, and J. R. Herkert. 2000. Egg rejection by cowbird hosts in grasslands. Auk 117:892–901.

Picman, J. 1989. Mechanism of increased puncture resistance of eggs of Brown-headed Cowbirds. Auk 106:577–583.

Rohwer, S. and C. D. Spaw. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird egg by old hosts. Evolutionary Ecology 2:27–36.

Rothstein, S. I. 1970. An experimental investigation of the defenses of the hosts of the parasitic Brown-headed Cowbird (*Molothrus ater*). Dissertation. Yale University, New Haven, Connecticut, USA.

Rothstein, S. I. 1975a. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

Rothstein, S. I. 1975b. Mechanisms of avian egg-recognition: do birds know their own eggs? Animal Behaviour 23:268–278.

Rothstein, S. I. 1978. Mechanisms of avian egg recognition: additional evidence for learned components. Animal Behaviour 26:671–677.

Rothstein, S. I. 1990. A model system for coevolution: avian brood parasitism. Annual Review of Ecology and Systematics 21:481–508.

Sealy, S. G. 1999. Cowbird parasitism on Lark Buntings: frequency, acceptance, and fledging. Journal of Field Ornithology 70:182–186.

Smith, J. N. M., T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy. (Editors). 2000. Ecology and management of cowbirds and their hosts: studies in the conservation of North American passerine birds. University of Texas Press, Austin, USA.

Underwood, T. J. and S. G. Sealy. 2002. Adaptive significance of egg coloration. Pages 280–298 *in* Avian incubation: behaviour, environment, and evolution (D. C. Deeming, Editor). Oxford University Press, Oxford, United Kingdom.

Underwood, T. J. and S. G. Sealy. 2006. Grasp-ejection in two small ejecters of cowbird eggs: a test of bill-size constraints and the evolutionary equilibrium hypothesis. Animal Behaviour 71:409–416.

Underwood, T. J. and S. G. Sealy. 2008. UV reflectance of eggs of Brown-headed Cowbirds (*Molothrus ater*) and accepter and rejecter hosts. Journal of Ornithology 149:313–321.

Zar, J. H. 1996. Biostatistical analysis. Third Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

The Wilson Journal of Ornithology 120(4):674–682, 2008

BETWEEN AND WITHIN CLUTCH VARIATION OF EGG SIZE IN GREATER RHEAS

GUSTAVO J. FERNÁNDEZ[1,2] AND JUAN C. REBOREDA[1]

ABSTRACT.—We describe egg characteristics, and analyze between and within clutch variation in egg size and mass in a natural population of Greater Rheas (*Rhea americana*). We assess the effect of this variation on nesting success and egg success. Yolk represented 29.5% of egg mass whereas albumen was 63.9%. Yolk mass increased with egg width but not with egg length, while mass of albumen increased mainly with egg length. The largest and smallest eggs were 10.3% larger and 25.3% smaller, respectively than mean intra-clutch values. The widest egg was 11.9% wider while the narrowest egg was 20.5% narrower than mean intra-clutch values. There was a significant decrease in egg size between clutches during the breeding season as a result of a decrease in egg length. There was no effect of laying order on intra-clutch variation in egg size, but we detected an increase in the variation of egg length within clutches with clutch size. We did not detect a relationship between egg size and nesting success, and between egg size and egg success. The relatively low intra-clutch variation in egg size and lack of effect of egg size on hatching success do not support the hypothesis that females invest in eggs according to expected chick fitness. *Received 23 November 2007. Accepted 15 April 2008.*

Intraspecific egg size variation is relatively common in birds (Slagsvold et al. 1984, Williams et al. 1993, Christians 2002). Most variation is among rather than within clutches and it is generally accepted this variation is the result of a strong genetic component of egg size (Christians 2002, Stryrsky et al. 2002, Valkama et al. 2002). However, variation among or within clutches laid by the same female should be attributed to phenotypic or environmental-mediated variation (Nager et al. 2006). Nutrient or energetic constraints could be responsible for egg size variation in some bird species (O'Connor 1979, Pierotti and Bellrose 1986). Egg size could also vary with parental age or experience with eggs laid by older and experienced females larger than those laid by younger females (Davis 1975, Blomqvist et al. 1997, Hipfner et al. 1997). Alternatively, egg size variation could respond to an adaptive investment of females, thereby influencing offspring quality. Larger eggs may contain more water and nutrients, which may benefit hatchlings by increasing their hatching success, growth rate, and survival (Parsons 1970, Reid and Boersma 1990, Magrath 1992, Williams 1994, Smith and Bruun 1998, Pelayo and Clark 2003). Egg size in some species decreases with laying order (e.g., Nisbet 1978, Shaw 1985, Custer and Frederick 1990). This decrease could be interpreted as an adaptive strategy because the reduction in size of last laid eggs could be a mechanism for shortening incubation period and favoring synchronous hatching (e.g., Birkhead and Nettleship 1982, Perrins 1996, Kennamer et al. 1997).

Maternal investment in eggs also could be related to mate quality or prospects of success. Some studies have found that females mated with non-preferred males produced fewer and smaller eggs than females mated with the males they chose (Yamamoto et al. 1989, Cunningham and Russell 2000).

Most studies of egg size variation were conducted on species where the clutch is laid by a unique female. In species with communal egg laying (where more than one female laid eggs into a single nest), differences in egg investment by females could have more important consequences for offspring fitness. For example, larger eggs in Guira Cuckoo (*Guira guira*) produce heavier and larger chicks that may out compete smaller and lighter nest companions (Macedo et al. 2004). As a consequence, larger communal clutches in this species had eggs with more nutrients than in smaller clutches. Females of species with communal laying could manipulate the nutrient investment in their eggs depending upon social condition to enhance individual fitness (Macedo et al. 2004).

We analyzed inter- and intra-clutch varia-

[1] Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón 2, Ciudad Universitaria, Buenos Aires, Argentina.

[2] Corresponding author; e-mail: gjf@ege.fcen.uba.ar

tion of egg size in a natural population of Greater Rheas (*Rhea americana*). Greater Rheas are communal nesters where two to 10 or more females lay eggs into a single nest that a male incubates. We analyzed the effect of season and clutch sizes (total number of eggs in the nest) on both inter- and intra-clutch variation of egg size to assess if egg size was associated with hatching success. The relationship between egg size and nesting success was analyzed because it is possible females reduce their investment in eggs laid for low quality males (i.e., young inexperienced or in poor physical condition) that are prone to desert the nest. We also analyzed the relationship between egg components (yolk and albumen) and egg size. We expected a positive relationship between egg size and yolk content, and between egg size and nest success, and hatching success.

METHODS

Study Site.—Data were collected during the 1992 and 1993 breeding seasons of Greater Rheas (Fernández and Reboreda 1998, 2003). We searched for Greater Rhea nests in three contiguous cattle ranches of ~3,500, 3,000, and 800 ha, near the town of General Lavalle in Buenos Aires Province, Argentina (36° 25′ S, 56° 56′ W). Numbers of rheas on these ranches were ~250, 100, and 150, respectively. The area is flat, low, and marshy with little of the land rising more than 10 m above sea level. Native vegetation is short grass with scattered patches of woodland in the higher areas (Fernández and Reboreda 1998).

Data Collection.—Greater Rhea nesting occurred from September to December, but most attempts were in November (Fernández and Reboreda 1998). We found 99 nests, 41 in 1992, and 58 in 1993. We used data from a sample of 53 active nests where we measured all eggs (30 nests in 1992, 23 in 1993). We individually numbered the eggs in each nest with water proof ink and recorded clutch size (number of eggs in the nest). Nests were visited (<20 min/visit) between 0900–1700 hrs every 2–3 days until the eggs hatched or the nest failed. We estimated the date at which laying started either directly (we knew the date of laying of the first egg) or indirectly by the color of the eggs (light yellow when laid but white in ~5 days) or by backdating (start of laying was estimated as date of hatching minus 40 days).

We measured length and width of the eggs with calipers (±0.1 mm) and mass with a 1-kg Pesola spring scale (±5 g). Egg mass varies during incubation (Grant et al. 1982) and we corrected it using the relationship between fresh egg weight and egg volume (length × width^2; Hoyt 1979) estimated from a subsample of 24 eggs found before onset of incubation. This relationship was highly significant ($F_{1,22} = 955.2$, $P < 0.0001$) and the model equation was:

$$\text{fresh mass (g)} = 11.8 + 0.55 \times (\text{length} \times \text{width}^2) \quad (R^2 = 0.98).$$

Egg volume was estimated using the water displacement for 39 fresh eggs collected from early deserted nests. We measured the volume displaced when the egg was immersed in water after its air cell was filled with water. The relationship between the product of L × W^2 (length × width^2) and the measured volume for these eggs was highly significant (simple regression analysis, $F_{1,37} = 101.6$, $P < 0.001$). The equation was:

$$\text{volume (cm}^3\text{)} = -47.18 + 0.56 \times (\text{L} \times \text{W}^2) \quad (R^2 = 0.73).$$

We collected fresh eggs from nests deserted before the onset of incubation to study egg composition. We took one egg from four nests and two eggs from another four nests (total = 12 eggs) to minimize pseudoreplication. Eggs were measured, weighed, and boiled for ~30 min to solidify the content (Carey 1996). We manually separated shell plus membranes, albumen, and yolk and recorded their wet mass with a Pesola spring scale (±5 g).

Statistical Analyses.—We estimated the variance component of differences in egg size (width and length) within and between clutches. We performed a one-way ANOVA, with egg measurements as dependent variables and nests as a random factor.

We assessed the relationship between laying sequence and egg size using simple regression analyses with transformed data. We standardized egg length and width dividing

each by the mean clutch value to correct for differences among clutches (Kennamer et al. 1997). We only included eggs laid up to 12 days after the start of laying.

We estimated intra-clutch variation in egg size by calculating the variation coefficients (CV) for each nest. We assessed variation of CVs with clutch size and season using general linear models (GLMs) with egg length and width as response variables, and season, clutch, and its interaction, as explanatory variables. We assigned nests to the date at which laying started and divided the breeding season into periods: 1–15 October; 16–31 October; 1–15 November; 16–30 November; 1–15 December; and 16–31 December. We did not observe laying after 31 December. We assumed a normal distribution of response variables, and checked it using residual and normal plots. We selected the final model after dropping all non-significant terms and checking for changes in deviance (Crawley 1993).

We used linear mixed models to test seasonal variation of egg size with egg length, width, and mass as response variables; year, clutch size, time of the season, and their second term interactions were explanatory variables. Nest identity was incorporated as a random factor to solve the problem of measuring eggs produced by the same female. We used residual and normal probability plots to check model assumptions. We selected the final model by sequentially dropping non-significant interactions and the non-significant main effects until only significant terms remained, and any additional factor deletion generated a significant change in the model. We assumed a normal distribution of residuals and used an identity link function for the analysis.

The wet mass of egg components (albumen, yolk, shell, and membranes) was related to egg total mass, volume, length, and width using simple regression analyses. Shell-free egg mass was estimated as the weight of the fresh egg minus the weight of the shell plus membranes. Yolk and albumen mass were expressed as the percentage of shell-free egg mass, whereas mass of shell and membranes was expressed as percentage of total weight of the fresh egg (including shell and membranes).

We evaluated differences in size and weight among eggs in successful and deserted nests using a generalized linear model (GLM) including year, season, clutch size, and mean egg volume as explanatory variables, and nest fate (successful or deserted) as the response variable. We assumed a binomial distribution of residuals for the response variable and a logit link function for this analysis. We used residual and normal probability plots to check model assumptions. We selected a final model by sequentially dropping non-significant interactions and then non-significant main effects until only significant terms remained (Crawley 1993). The effect of egg characteristics on probability of hatching was tested using a logit regression with a binary response (hatched-non-hatched) and egg length, egg width, and season as independent variables. Egg length and width were standardized to the mean value of each nest. Hatching success can vary with egg size in a non-linear form (Deeming 1995), and we included the quadratic terms for egg width and length as predictor variables in an alternative model. We used Genstat DE2 (Release 4.2, VSN International Ltd., UK) to fit the models and perform all statistical analyses. All statistics presented are two-tailed and measures are mean ± SD.

RESULTS

Egg Size Variation.—We measured 1,226 Greater Rhea eggs from 53 nests. Egg volume varied from 255.4 to 788.0 cm^3 and egg mass from 275 to 825 g (Table 1). Egg length was more variable than egg width (Table 1). The largest egg was 10.3% larger while the smallest egg was 25.3% smaller than mean values. The widest egg was 11.9% wider while the narrowest egg was 20.5% narrower than mean values. Within clutch variation of egg width was higher than between clutch variation, while variation of egg length was similar within and between clutches. The variance in egg width explained by within clutch variation was 80.8%, whereas variance explained by between-clutches variation was 19.2%. Similarly, variation in egg length explained by within clutch variation was 88.7%, while between clutches variation only explained 11.3% of the variance.

Variation in egg length within clutches was related to clutch size (variance ratio $VR_{11,48}$ = 2.18, P = 0.04) but was independent from time of the season (ΔD = 5.43, df = 4, P = 0.02 for clutch size; and $P > 0.05$ for time of

TABLE 1. Morphological characteristics of Greater Rhea eggs from 53 nests (mean clutch size = 22.6 eggs, SD = 10, range = 7–56 eggs), Buenos Aires Province, Argentina.

	Mean	SD	Range	*n*
Length (cm)	13.3	0.55	9.9–14.6	1,226
Width (cm)	9.3	0.38	7.39–10.4	1,225
Mass (g)	618.7	65.1	275–825	1,113
Volume (cm^3)	595.4	66.5	255.4–788.0	1,125
Density (g/cm^3)[a]	1.0	0.06	0.75–1.3	1,107
Area (cm^2)[b]	340.3	24.0	199.2–412.2	1,113
Shell density (g/cm^3)[c]	2.1	0.003	2.1–2.1	1,113

[a] Density = 1.038 × $weight^{0.006}$ (Paganelli et al. 1974).
[b] Area = 4.835 × $weight^{0.662}$ (Paganelli et al. 1974).
[c] Shell density = 1.945 × $weight^{0.014}$ (Paganelli et al. 1974).

the season and the interaction term). The coefficient of variation in egg length increased with clutch size. In contrast, within-clutch variation in egg width did not vary with clutch size or season (variance ratio $VR_{11,48} = 0.67$, $P = 0.75$).

Egg Composition.—Yolk mass represented 29.5 ± 3.5% ($n = 11$, range = 24.1–35.6%) of egg mass and 34.7 ± 3.4% (range = 29.5–42.5%) of shell-free egg mass. Mean yolk mass was 170 ± 18.1 g and varied linearly with egg mass ($F_{1,10} = 10.9$, $P = 0.01$, $R^2 = 0.58$), and egg volume ($F_{1,10} = 13.2$, $P = 0.04$, $R^2 = 0.34$; Fig. 1). Yolk mass increased with egg width (regression analysis, $F_{1,10} = 13.2$, $P = 0.005$, $R^2 = 0.57$), but was independent of egg length (regression analysis, $F_{1,10} = 0.135$, $P = 0.72$).

Albumen mass represented 63.9 ± 3.5% ($n = 10$, range = 51.7–70.5 %) of egg mass and 66 ± 2.4% (range = 61.3–70.5%) of shell-free egg mass. Mean albumen mass was 330.5 ± 28.3 g and increased with egg length, width, mass, and volume (regression analyses; $F_{1,8} = 7.23$, $P = 0.03$, $R^2 = 0.47$; $F_{1,8} = 5.31$, $P = 0.05$, $R^2 = 0.32$; $F_{1,8} = 18.7$, $P = 0.002$, $R^2 = 0.64$; and $F_{1,8} = 37.9$, $P < 0.01$, $R^2 = 0.83$, respectively; Fig. 1). We did not detect a relationship between albumen and yolk mass (Pearson product-moment correlation, $r = 0.42$, $P > 0.05$).

Mean mass of shell and membranes was 84.0 ± 15.1 g and represented 14.5 ± 2.4% of egg mass (range = 11.8–19.6%). We did not find any relationship among mass of shell plus membranes and egg mass, volume, length or width (regression analyses, $P > 0.05$).

Effect of Laying Order and Time of Breeding on Egg Characteristics.—We found no effect of laying order on egg length ($F_{1,136} = 1.54$, $P = 0.22$), egg width ($F_{1,136} = 0.13$, $P = 0.72$), and egg mass ($F_{1,136} = 0.81$, $P = 0.37$). Similarly, egg characteristics were not affected by clutch size ($F_{1,35} = 1.45$, $P = 0.24$ for length; $F_{1,35} = 0.74$, $P = 0.39$ for breadth; $F_{1,35} = 0.05$, $P = 0.82$ for mass).

The minimal model for explaining between-clutch variation of egg length included season and the interaction between year and season (*Wald*/df = 3.74, df = 5, $P = 0.002$, and *Wald*/df = 2.67, df = 4, $P = 0.03$, respectively). Egg length decreased towards the end of the breeding season (Dec), but this decrease was most important during 1992 (Fig. 2A). We did not detect any effect of season, clutch size, and year on egg width (Fig. 2B). Egg mass had a significant decrease with time of breeding, and the interaction between year and time of breeding (*Wald*/df = 2.80, df = 5, $P = 0.02$, and *Wald*/df = 3.31, df = 3, $P = 0.02$, respectively). Egg mass also decreased towards the end of the breeding season and the decrease was most prominent during 1992.

Effect of Egg Size on Nest Fate and Hatching success.—Mean egg size, clutch size, and season did not affect nest fate (*Deviance ratio* = 0.84, $df_{reg} = 8$, $df_{res} = 29$, $P = 0.57$). Successful and deserted nests had similar mean egg sizes (*t*-test, *a posteriori*, $t_{37} = -0.05$, $P = 0.96$). Hatching success was not affected by egg size ($\Delta D = 0.77$, df = 1, $P = 0.39$) but was affected by season ($\Delta D = 5.43$, df = 4, $P = 0.01$) although it does not vary in a predictable manner (simple regression, $F_{1,20} = 0.015$, $P = 0.90$).

DISCUSSION

Egg Size Variation.—Eggs of Greater Rheas varied considerably in size, differing in

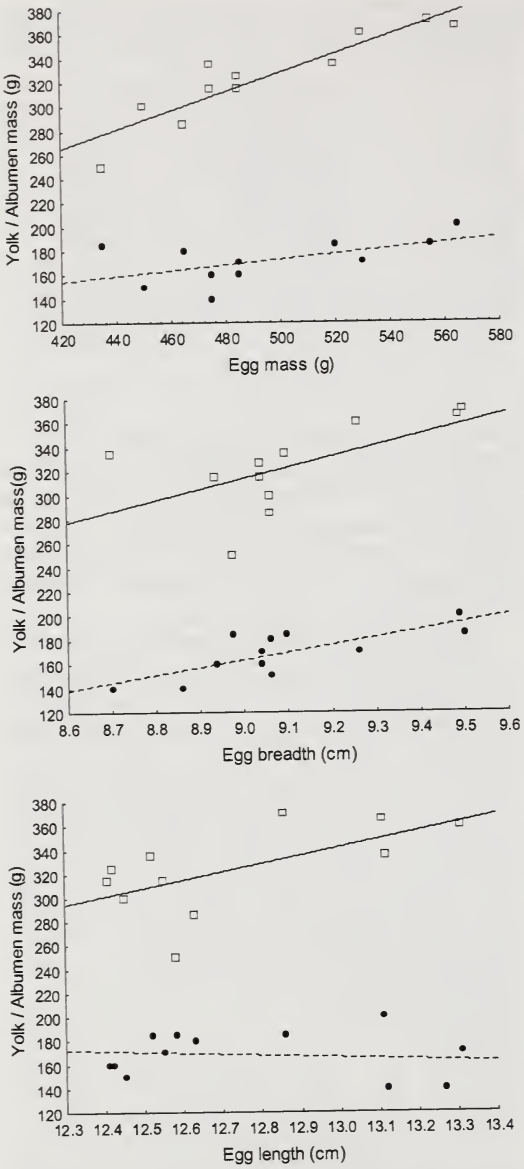


FIG. 1. Variation of yolk and albumen mass with egg mass, egg length, and egg width. Full lines represent adjusted functions for albumen mass variation with these independent variables, whereas broken lines represent the adjusted functions for variation in yolk mass.

mass by up to 550 g. Egg length and width also varied, as the largest rhea egg was 148% larger than the smallest, while the widest egg was 140% wider than the most narrow one.

We detected differences in egg size between clutches associated with date of egg laying. There was a significant reduction in egg length but not in egg width during the breeding season. Other authors also found a negative association between egg size and laying date (i.e., Coulson and White 1958, Furness 1983, but see Perrins 1996). The reduction in egg size could affect embryo development and hatching success (Dzialowski and Sotherland 2004) or post-fledgling survival (Dow and Fredga 1984, Newton and Marquiss 1984, Dzus and Clark 1998, but see Blomqvist et al. 1997 and Massaro et al. 2002). We did not detect differences in a previous study in short-term survival between chicks hatched early (Nov-Dec) and late in the breeding seasons (Jan-Feb) (Fernández and Reboreda 2003). The lack of differences in egg size between successful and failed nests, and the absence of effects of egg size on the probability of hatching appear to indicate that seasonal reduction in egg size in Greater Rheas does not affect female fitness.

The decline in egg size could be the consequence of female differences in age and/or experience. Some authors have reported the ability of females to produce eggs improves with age, resulting in older females laying earlier and larger eggs (Hipfner et al. 1997, Massaro et al. 2002). Similarly, eggs laid by young Greater Rhea females in captivity are smaller than those laid by older, experienced females (Flieg 1973, Guittin 1985, Gunski 1992). Besides, nesting success increases during the breeding season (Fernández and Reboreda 1998). Therefore, young females would be expected to have higher fitness than older hens if the differences in egg size we found were age related.

Another hypothesis for explaining seasonal variation in egg size postulates that females are constrained by laying late in the season (Lack 1968). Food supply, nutrient availability, or body reserves late in the season could affect the capability of females for laying (Williams 1994, 2005). In a related species, Emu (*Dromaius novaehollandiae*), clutch size appears to vary with amount of food available before laying (Davies 2002). Polyandry in rheas could similarly increase female demand for nutrients as the breeding season advances, limiting female capability for egg synthesis. Constraints in food quality or supply could af-

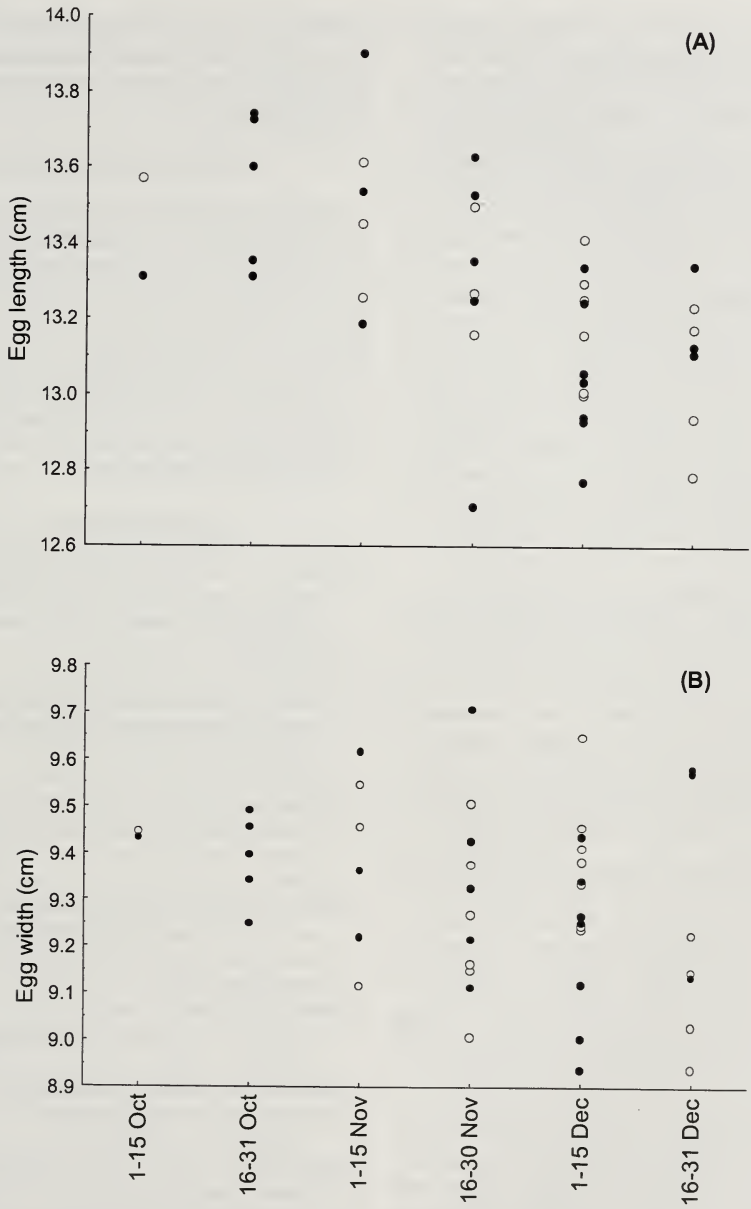


FIG. 2. Seasonal variation in egg length (A), and width (B) in Greater Rheas. Open and black dots correspond to egg mean values for clutches measured during 1992 and 1993, respectively.

fect egg size without affecting hatching success and chick survival.

We found that intra-clutch variation of egg size increased with clutch size. This variation could reflect the mating system of rheas. In this species, males defend a group of females that lay their eggs communally in a single nest. Thus, the variation detected may be the consequence of a larger number of different females laying their eggs in the same nest, as larger clutches are the result of larger harems laying in the same nest (Fernández and Reboreda 1998).

Egg Content and Egg Size Variation.—Yolk mass represented ~35% of egg content. This value was slightly smaller than predicted (39.1) for precocial eggs using the equation of Sotherland and Rahn (1987). It was similar to

that measured in Common Ostrich (*Struthio camelus*, 37.8%; Sotherland and Rahn 1987), but smaller than that of Southern Cassowary (*Casuarius casuarius*, 42%; Sotherland and Rahn 1987), Emu (47%; Dzialowski and Sotherland 2004), and Southern Brown Kiwi (*Apteryx australis*, 61%; Calder et al. 1978). The smaller content of yolk mass in rhea eggs is associated with a shorter incubation period (40 days) compared to other ratites (Emu: 56 days; Cassowary: 50–52 days; Kiwi: 70–90 days; Davis 2002) but similar to that of ostriches (40–45 days). The percentage of yolk mass of rheas that we measured was similar to that obtained in a previous study with eggs collected in captive and wild populations (Navarro et al. 2001). That study found that wet yolk represented ~34–36% of shell-free egg mass.

Seasonal reduction in egg length and the increase in egg size differences within clutches as clutch size increases were not associated with changes in yolk content, but likely with albumen mass, as the latter was associated with egg length. Females under nutritional constraints may reduce investment by reducing albumen content, while keeping yolk content constant. If natural selection favors reduction in variation of egg characteristics that affect chick fitness (Jover et al. 1993), females with nutritional constraints could vary investment in egg components other than yolk content (Carey et al. 1980). Thus, it would be expected that lower seasonal variation in egg width (which is associated with yolk content) than in egg length (which is associated with albumin content) would produce no effect on egg size on hatching success. Additional support is provided by the absence of an association between variation in egg width and clutch size, which could reflect the high constancy of yolk contained within eggs.

Variation of egg size in Greater Rheas was not associated with a decrease in hatching success or nesting success. Thus, there are no apparent benefits from laying larger eggs, as reported for other precocial species (i.e., Hepp et al. 1989). Seasonal variation of egg size in Greater Rheas would be the result of environmental constraints (nutrients or food quality or availability) and/or variation in quality, age or experience of laying females, rather than an adaptive strategy of females to maximize hatching success and chick survival. Further data about nutritional constraints and female investment in eggs are necessary to confirm this hypothesis.

ACKNOWLEDGMENTS

We thank John Boote and Horacio Martínez Guerrero for allowing us to conduct this study at Estancias Los Yngleses and La Clementina, respectively, and Raúl Paso, José Flores, and Angel Guzmán for their field collaboration. Myriam Mermoz, Fernando Lorenzini, and Silvia Rossi helped at different stages of field work. Mario Beade from Fundación Vida Silvestre Argentina provided logistical support during the field work. GJF and JCR are research fellows of Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET).

LITERATURE CITED

Birkhead, T. R. and D. N. Nettleship. 1982. The adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. Ecology 63: 300–306.

Blomqvist, D., O. C. Johansson, and F. Götmark. 1997. Parental quality and egg size affect chick survival in a precocial bird, the Lapwing *Vanellus vanellus*. Oecologia 110:18–24.

Calder, W. A., C. R. Parr, and D. P. Karl. 1978. Energy content of eggs of the Brown Kiwi *Apteryx australis*: an extreme in avian evolution. Comparative Biochemistry and Physiology 60:177–179.

Carey, C. 1996. Female reproductive energetics. Pages 324–375 *in* Avian energetics and nutritional ecology (C. Carey, Editor). Chapman and Hall, New York, USA.

Carey, C., H. Rahn, and P. Parisi. 1980. Calories, water, lipid and yolk in avian eggs. Condor 82: 335–343.

Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. Biological Reviews 77:1–26.

Coulson, J. C. and E. White. 1958. The effect of age on the breeding biology of the Kittiwake *Rissa tridactyla*. Ibis 100:40–51.

Crawley, M. 1993. Glim for ecologists. Blackwell Scientific Publishing, Oxford, United Kingdom.

Cunningham, E. J. A. and A. F. Russell. 2000. Egg investment is influenced by male attractiveness in the Mallard. Nature 404:74–76.

Custer, T. W. and P. C. Frederick. 1990. Egg size and laying order of Snowy Egrets, Great Egrets, and Black-crowned Night-herons. Condor 92: 772–775.

Davis, J. W. F. 1975. Age, egg size and breeding success in the Herring Gull *Larus argentatus*. Ibis 117:460–473.

Davis, S. J. J. F. 2002. Ratites and tinamous. Oxford Unversity Press, New York, USA.

Deeming, D. C. 1995. Factors affecting hatchability during commercial incubation of Ostrich (*Struthio camelus*) eggs. British Poultry Science 36:51–56.

Dow, H. and S. Fredga. 1984. Factors affecting reproductive output of the golden-eye duck *Bucephala clangula*. Journal of Animal Ecology 53: 679–692.

Dzialowski, E. M. and P. R. Sotherland. 2004. Maternal effects of egg size on Emu *Dromaius novaehollandiae* egg composition and hatchling phenotype. Journal of Experimental Biology 207: 597–606.

Dzus, E. H. and R. G. Clark. 1998. Brood survival and recruitment of Mallard in relation to wetland density and hatching date. Auk 115:311–318.

Fernández, G. J. and J. C. Reboreda. 1998. Effects of clutch size and timing of breeding on reproductive success of Greater Rheas. Auk 115:340–348.

Fernández, G. J. and J. C. Reboreda. 2003. Male parental care in Greater Rheas (*Rhea americana*) in Argentina. Auk 120:418–428.

Flieg, G. M. 1973. Nutritional problems in young ratites. International Zoo Yearbook 13:158–163.

Furness, R. W. 1983. Variations in size and growth of Great Skua *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. Journal of Zoology 199: 101–116.

Grant, G. S., C. V. Paganelli, T. N. Petit, G. C. Whittow, and H. Rahn. 1982. Determination of fresh egg mass during natural incubation. Condor 84:121–122.

Guittin, P. 1985. Les strutioniformes en parc zoologique, reproduction, croissance, élevage. These de Doctorat. Université Paris, France.

Gunski, R. J. 1992. Análise citogenética e algunas consideraçoes biológicas da espécie *Rhea americana* - ema (aves:Rheidae). Thesis. Facultad de Ciencias Agrarias y Veterinaria. Universidad Estadual Paulista, Sao Paulo, Brasil.

Hepp, G. R., R. A. Kennamer, and W. F. Harvey. 1989. Recruitment and natal philopatry of Wood Ducks. Ecology 70:897–903.

Hipfner, J. M., A. J. Gaston, and L. N. D. Forest. 1997. The role of female age in determining egg size and laying date of Thick-billed Murres. Journal of Avian Biology 28:271–278.

Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73–77.

Jover, L., X. Ruiz, and M. González-Martín. 1993. Significance of intraclutch egg size variation in the Purple Heron. Ornis Scandinavica 24:127–134.

Kennamer, R., S. K. Alsum, and S. V. Colwell. 1997. Composition of Wood Duck eggs in relation to egg size, laying sequence, and skipped days of laying. Auk 114:479–487.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, United Kingdom.

Macedo, R. H. F., M. O. Cariello, A. M. Pacheco, and H. G. Schwabl. 2004. Significance of social parameters on differential nutrient investment in Guira Cuckoo (*Guira guira*) eggs. Animal Behaviour 68:685–694.

Magrath, R. D. 1992. The effect of egg mass on the growth and survival of Blackbirds: a field experiment. Journal of Zoology 227:639–653.

Massaro, M., J. T. Darby, L. S. Davis, K-A. Edge, and M. J. Hazel. 2002. Investigation of interacting effects of female age, laying dates, and egg size in Yellow-eyed Penguins (*Megadyptes antipodes*). Auk 119:1137–1141.

Nager, R. G., P. Monaghan, D. C. Houston, K. E. Arnold, J. D. Blount, and N. Verboven. 2006. Maternal effects through the avian egg. Acta Zoologica Sinica 52(Supplement):658–661.

Navarro, J. L., M. L. López, D. M. Maestri, and D. O. Labuckas. 2001. Physical characteristics and chemical composition of Greater Rhea (*Rhea americana*) eggs from wild and captive populations. British Poultry Science 42:658–662.

Newton, I. and M. Marquiss. 1984. Seasonal trend in the breeding performance of Sparrowhawks. Journal of Animal Ecology 53:809–829.

Nisbet, I. C. T. 1978. Dependence of fledging success on egg size, parental performance and egg composition among Common and Roseate terns, *Sterna hirundo* and *S. dougallii*. Ibis 120:207–215.

O'Connor, R. J. 1979. Egg weight and brood reduction in the European Swift (*Apus apus*). Condor 81:133–145.

Paganelli, C., A. Oliszowka, and A. Ar. 1974. The avian egg: surface area, volume, and density. Condor 76:319–325.

Parsons, J. 1970. Relationship between egg size and posthatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228:1221–1222.

Pelayo, J. T. and R. G. Clark. 2003. Consequences of egg size for offspring survival: a cross-fostering experiment in Ruddy Ducks (*Oxyura jamaicensis*). Auk 102:384–393.

Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. Ibis 138:2–15.

Pierotti, R. and C. A. Bellrose. 1986. Proximate and ultimate causation of egg size and the "third-chick disadvantage" in the Western Gull. Auk 103:401–407.

Reid, W. V. and P. D. Boersma. 1990. Parental quality and selection on egg size in the Magellanic Penguin. Evolution 44:1780–1786.

Shaw, P. 1985. Brood reduction in the Blue-eyed Shag *Phalacrocorax atriceps*. Ibis 127:476–494.

Slagsvold, T., J. Sandvick, G. Rofstad, Ö. Lorentsen, and M. Husby. 1984. On the adaptive value of intraclutch egg-size variation in birds. Auk 101: 685–697.

Smith, H. G. and M. Bruun. 1998. The effect of egg size and habitat on Starling nestling growth and survival. Oecologia 115:59–63.

Sotherland, P. R. and H. Rahn. 1987. On the composition of bird eggs. Condor 89:48–65.

Styrsky, J. D., R. C. Dobbs, and C. F. Thompson. 2002. Sources of egg-size variation in House Wrens (*Troglodytes aedon*): ontogenetic and environmental components. Auk 119:800–807.

Valkama, J., E. Korpimäcki, J. Wiehn, and T. Pakkanen. 2002. Inter-clutch egg size variation in Kestrels *Falco tinnunculus*: seasonal decline under fluctuating food conditions. Journal of Avian Biology 33:426–432.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biological Review 68:35–59.

Williams, T. D. 2005. Mechanisms underlying the costs of egg production. Bioscience 55:39–48.

Williams, T. D., D. B. Lank, and F. Cooke. 1993. Is intraclutch egg-size variation adaptive in the Lesser Snow Goose? Oikos 67:250–256.

Yamamoto, J. T., K. M. Shields, J. R. Milliam, T. E. Roudybush, and C. R. Grau. 1989. Reproductive activity of forced paired Cockatiels (*Nymphicus hollandicus*). Auk 106:86–93.

The Wilson Journal of Ornithology 120(4):683–691, 2008

DNA SEQUENCE ASSESSMENT OF PHYLOGENETIC RELATIONSHIPS AMONG NEW WORLD MARTINS (HIRUNDINIDAE: *PROGNE*)

ROBERT G. MOYLE,[1] BETH SLIKAS,[2] LINDA A. WHITTINGHAM,[3] DAVID W. WINKLER,[4] AND FREDERICK H. SHELDON[5,6]

ABSTRACT.—The classification of New World martins (*Progne*) has a convoluted history because taxonomists have relied on plumage traits that vary continuously across populations. We estimated the phylogeny of *Progne* by analyzing mitochondrial cytochrome *b* DNA sequences of 27 individuals of eight of the nine species (10 subspecies) and nuclear β-fibrinogen intron 7 sequences of 20 individuals of six species (8 subspecies). The Brown-chested Martin (*P. tapera*) is sister to other *Progne* species. The Middle American taxa—Sinaloa Martin (*P. sinaloae*), Cuban Martin (*P. cryptoleuca*), Caribbean Martin (*P. dominicensis*), and Central American populations of Gray-breasted Martin (*P. chalybea*)—form a well supported clade. This group is distinct from Purple Martin (*P. subis*), which has no particularly close relatives. All four Middle American taxa appear to be good species, although Cuban and Caribbean martins could be merged in view of their similar plumage and low genetic divergence (1.2%). Two of the South American taxa, the Peruvian Martin (*P. murphyi*) and Southern Martin (*P. elegans*), are also distinct species. We did not examine the Galapagos Martin (*P. modesta*) for lack of DNA, but it is likely to be a good species as well. An unexpected result of the study was that Gray-breasted Martin appears polyphyletic; its South American populations are closer to the Southern Martin than to its Central American populations. *Received 4 September 2007. Accepted 1 February 2008.*

The New World martins are large, generally bluish or brownish swallows that range from Canada to southern Argentina. All taxa are morphologically similar and their plumages often grade into one another. Thus, the group's classification is unsettled with names of species and subspecies having been shuffled in numerous ways to convey presumed relationships. Current classifications (AOU 1998, Dickinson 2003) generally group the martins in a single genus (*Progne*) consisting of nine species: *P. tapera* (Brown-chested Martin), *P. subis* (Purple Martin), *P. cryptoleuca* (Cuban Martin), *P. dominicensis* (Caribbean Martin), *P. sinaloae* (Sinaloa Martin), *P. chalybea* (Gray-breasted Martin), *P. modesta* (Galapagos Martin), *P. elegans* (Southern Martin), and *P. murphyi* (Peruvian Martin). This classification facilitates discussion of the martins, but it conveys no phylogenetic structure and does not necessarily indicate appropriate species boundaries.

At the generic level, the martins have been grouped in either *Progne* (Peters 1960, AOU 1998, Dickinson 2003, Turner 2004) or divided between *Progne* and *Phaeoprogne* (Sibley and Monroe 1990). When recognized, *Phaeoprogne* consists of one species, Brown-chested Martin, which is distinguished from all other New World martins by its lack of iridescence and sexual dimorphism, and its shorter and less forked tail (Turner 2004). Brown-chested Martin is also genetically distinct from other martin species, although within range of a typical passerine congener (Sheldon and Winkler 1993, Whittingham et al. 2002).

Classification of the eight remaining species of martins (*Progne* sensu stricto) is unsettled. Their largely allopatric distributions and similar plumages have caused several authors to suggest these taxa might constitute a single polytypic species (Hellmayr 1935, Short 1975), but they have not been so classified. Some taxonomists have recognized four species (Peters 1960, Turner 2004): *P. subis*

[1] Natural History Museum and Biodiversity Research Center, and Department of Ecology and Evolutionary Biology, University of Kansas, Dyche Hall, Lawrence, KS 66045, USA.

[2] Blood Systems Research Institute, 270 Masonic Avenue, San Francisco, CA 94118, USA.

[3] Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI 53201, USA.

[4] Cornell University Museum of Vertebrates, Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA.

[5] Museum of Natural Science and Department of Biological Sciences, 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA.

[6] Corresponding author; e-mail: fsheld@lsu.edu

(North America), *P. dominicensis* (Mexico and Caribbean, including *dominicensis*, *cryptoleuca*, and *sinaloae*), *P. chalybea* (Central and South America), and *P. modesta* (South America and Galapagos). This arrangement emphasizes male plumage in defining species. *P. dominicensis* males are dark blue with white bellies. *P. chalybea* males have blue upperparts and light underparts with a gray or bluish-gray throat. *P. subis* and *P. modesta* males are both entirely blue, but female *P. subis* are lighter than the chocolate-colored female of *P. modesta*.

Particular confusion has surrounded the relationships among the North and Middle American species. Hellmayr (1935) treated Caribbean *cryptoleuca* and *dominicensis* as subspecies of North American *P. subis*. He argued that plumages of these taxa grade into one another, Cuban *cryptoleuca* being intermediate between *dominicensis* and *P. subis* in the amount of white in its belly. He recognized *P. sinaloae* as a full species. Zimmer (1955) and Eisenmann (1959) believed that *sinaloae*, *cryptoleuca*, and *dominicensis* should be united in a single species based on the possession of a white belly and also because they form a link between the North American *P. subis* and Central and South American *P. chalybea*. Zimmer (1955) noted that although male *cryptoleuca* resemble male *P. subis*, female *cryptoleuca* more closely resemble female *P. chalybea*. Phillips (1986) formalized these arguments by grouping *cryptoleuca*, *dominicensis*, and *sinaloae* in a single species, *P. dominicensis* (Snowy-bellied Martin). This arrangement divided the North and Central American taxa into three distinct units, *P. subis*, *P. dominicensis*, and *P. chalybea*. The cohesiveness of this group was emphasized by Sibley and Monroe (1990) in designating the superspecies *P. subis*.

Uncertainty also surrounds the "southern martins": *P. modesta* (Galapagos), *P. murphyi* (north coastal Peru), and *P. elegans* (east of the Andes). Observations on their relationships are relatively few in comparison to northern taxa because less is known about them. Hellmayr (1935), Zimmer (1955), Sibley and Monroe (1990), and Turner (2004) merged the three into *P. modesta*, but the AOU (1998) kept them as distinct species (also see Dickinson 2003). The taxa resemble one another with the centrally located *P. murphyi* somewhat intermediate in plumage (Turner 2004). *P. elegans* is larger than *P. modesta* and *P. murphyi* and has more white in the female plumage, especially on the forehead (Short 1975). The disjunct distribution of the southern martins begs the question of how they evolved. They might be isolated and diverging populations of a single, once widespread species, or they might be independently founded populations of northern taxa. An interesting clue, or complication, is that breeding ranges of *P. elegans* and *P. chalybea* overlap in the southern Chaco, and the two hybridize there (Eisenmann and Haverschmidt 1970, Short 1975).

We reconstructed the intrageneric phylogeny of New World martins using DNA sequence data. The purposes of the study were to examine (1) whether the martins are divided into clearly defined clades that may be considered species, and (2) how these clades are related to one another. Knowledge of *Progne* phylogeny, in combination with geographic and plumage data, would provide the foundation for a stable classification useful to the many ecologists and behaviorists who study these birds. It would also provide the framework for future studies of population genetics of the genus.

METHODS

Martin phylogeny was estimated by comparing mitochondrial cytochrome *b* (cytb) and nuclear β-fibrinogen intron 7 (βfib7) DNA sequences (Table 1). DNA of most species was extracted from preserved tissues, but museum skins served as the source of DNA for *P. sinaloae*, *P. murphyi*, and *P. modesta*. Swallows closely related to martins served as outgroups (Sheldon et al. 2005). These included Southern Rough-winged Swallow (*Stelgidopteryx ruficollis*), White-banded Swallow (*Atticora fasciata*), Blue-and-white Swallow (*Pygochelidon cyanoleuca*), and Golden Swallow (*Tachycineta euchrysea*).

Genomic DNA was extracted from preserved tissue using the phenol/chloroform extraction method (Hillis et al. 1990, Slikas et al. 2000). DNA from museum skins was extracted in a designated ancient DNA laboratory and stringent precautions were followed to avoid contamination. All surfaces were

TABLE 1. List of taxa, specimens, and localities compared.

Species[a]	Sample[b] #	Cytb length	Cytb GenBank #	βFib7 length	βFib7 GenBank #	Locality
Progne tapera (Brown-chested Martin)	B7297	955	AF074588	856	AY827412	Loreto Department, Peru
P. subis subis (Purple Martin)	B25082	913	AY825996	855	AY827413	East Baton Rouge Parish, LA, USA
	B25083	863	EU427735	435	Y827413	East Baton Rouge Parish
	B5866	996	EU427734	435	EU427759	Cameron Parish
	B30441	996	EU427733	435	EU427758	Cameron Parish
	B45004	863	EU427736	855	EU427755	Timbalier Islands, LA, USA
	B45475	996	EU427742	856	EU427754	Amazonas, Brazil
P. subis arboricola (Purple Martin)	B41548	996	EU427731	435	EU427757	Grant County, NM, USA
	B41549	996	EU427732	435	EU427756	Grant County
	AB	996	EU427730			Maplewood, BC, Canada
	B38690	996	EU427745			Riverside County, CA, USA
P. cryptoleuca (Cuban Martin)	B52873	973	AY825945	856	EU427760	Cuba
P. dominicensis (Caribbean Martin)	B22019	951	AY825946	856	AY827415	Dominican Republic
P. sinaloae (Sinaloa Martin)	KMNH 40044*	537	AY825947			Sinaloa, Mexico
	KMNH 40045*	537	EU427740			Sinaloa, Mexico
P. chalybea chalybea (Gray-breasted Martin)	B28808	995	AY825948	856	EU427750	Panama Province, Panama
	B28806	996	EU427738	856	EU427749	Panama Province
	B27272	995	EU427737			Alajuela Province, Costa Rica
	B9486	939	AF074583	856	AY827416	Pondo Department, Bolivia
	B9562	995	EU427739	856	EU427753	Pondo Department
	B7366	995	EU427740	856	EU427752	Loreto Department, Peru
P. chalybea macrorhamphus (Gray-breasted Martin)	B15315	996	EU427741	435	EU427760	Santa Cruz Department, Bolivia
P. elegans (Southern Martin)	B25506	996	AY825949	856	AY827417	Amazonas, Brazil (austral migrant)
	PRS1690	996	EU427743	435	EU427761	Anelo Department, Argentina
	PRS1758	996	EU427744	856	EU427748	Anelo Department
P. murphyi (Peruvian Martin)	LSUMZ 114184*	891	EU427746			Arequipa Department, Peru
	LSUMZ 114186*	891	AY825950			Arequipa Department, Peru
Tachycineta euchrysea (Golden Swallow)	B22018	969	AY052451	856	AY827409	Dominican Republic
Atticora fasciata (White-banded Swallow)	B12682	900	AF074584	856	AY827427	Santa Cruz Department, Bolivia
Pygochelidon cyanoleuca (Blue-and-white Swallow)	B12191	906	AF074586	857	AY826003	Pichincha Province, Ecuador
Stelgidopteryx ruficollis (Southern Rough-winged Swallow)	B1130	901	AF074589	856	AY827411	La Paz Department, Bolivia

[a] Classification follows AOU (1998) and Dickinson (2003).

[b] AB, Allan Baker, Royal Ontario Museum; B, Louisiana State Museum of Natural Science Collection of Genetic Resources; KMNH, Kansas University Museum of Natural History; LSUMZ, LSU Museum of Natural Science Bird Collection; PRS, Paul Sweet, American Museum of Natural History. *DNA extracted from museum skin.

TABLE 2. Primers used for DNA amplification and sequencing.

Primer	Sequence (5′-3′)	Source
Cyt *b*		
H16065	GGAGTCTTCAGTCTCTGGTTTACAAGAC	Helm-Bychowski and Cracraft (1993)
H15710	GTAGGCGAATAGGAAGTATC	Helm-Bychowski and Cracraft (1993)
CBINT	GGTTGTTTGAGCCGGATTC	Avise et al. (1994)
L15656	AACCTACTAGGAGACCCAGA	Helm-Bychowski and Cracraft (1993)
L14993	CCATCCAACATCTCAGCCTGATGAAACTT	Modified from Kocher et al. (1989)
L14999	CTCATCTTGATGAAACTTCGGATC	Modified from Kocher et al. (1989)
L15191	ATCTGCATCTACCTACACATCGG	Modified from Kocher et al. (1989)
L15311	GCAAGCTTCTACCATGAGGACAAATATC	Modified from Kocher et al. (1989)
cytbC	CAAGCTTCTACCATGAGGAC	Modified from Kocher et al. (1989)
L15719	AAACCCGAATGATACTTCCT	Modified from Kocher et al. (1989)
H15331	AAACTGCAGCCCCTCAGAATGATATTT	Modified from Kocher et al. (1989)
cytbE	ATAGGAAGTATCATTCGGGT	Modified from Kocher et al. (1989)
βFib7		
FIB-BI7L	TCCCCAGTAGTATCTGCCATTAGGGTT	Prychitko and Moore (1997)
FIB-BI7U	GGAGAAAACAGGACAATGACAATTCAC	Prychitko and Moore (1997)
FIB-BI7Lb	CAGTGCTCTATTATGTACTTTAC	Sheldon et al. (2005)
FIB-BI7Ub	TGGGTCCTGAAGAAAGAGGC	Sheldon et al. (2005)

cleaned with 10% bleach solution prior to extractions. Pipettors were cleaned with bleach solution following each set of extractions and filter-tips were used. All reagents were exposed to UV light (254 nm) for at least 20 min prior to use. Gloves, lab coat, and face mask were worn at all times during extraction and PCR preparation. DNA was extracted in sets of six, including five samples and a blank extraction control. Samples were first chopped finely with a sterile scalpel blade, then added to 750 μl of digestion buffer (10 mg/ml DTT, 1 mg/ml Proteinase K, 1% SDS, 10 mM Tris, 2 mM EDTA, 10 mM $NaCl_2$) and incubated overnight in an oven at 55° C in a rotating stand. Each sample was purified with two phenol and a single chloroform extraction following digestion. Each supernatant was washed with sterile, UV-treated H_2O and concentrated using Centricon 30 columns (Amicon Inc., Beverly, MA, USA). Each sample was brought to a final volume of 120–160 μl with sterile, UV-treated H_2O, aliquoted into four tubes of equal volume and heated at 65° C in a heat block for 10 min (to remove DNAse). Extracted DNA was stored in a −20° C freezer in the ancient DNA laboratory. PCR reactions were prepared in an ancient DNA laboratory, but PCR amplification and post-PCR procedures were performed in the primary genetics laboratory. Amplification and sequencing from skin specimens was done piecewise in fragments ranging from 150 to 400 base pairs.

All DNA was sequenced in both directions using the primers (listed in Table 2) and either a Product Sequencing Kit (Version 2.0, U. S. Biochemical, Cleveland, OH, USA), or standard cycle sequencing. DNA was sequenced either by hand on a 6% polyacrylamide gel or with an ABI 373 or ABI 3100 automated sequencer. A maximum of 996 nucleotides of cytb, spanning sites 15046 to 16041 in the chicken mitochondrial genome (Desjardins and Morais 1990), was sequenced (Table 1). Shorter sequences were obtained for taxa whose DNA was extracted from museum skins. βfib7 lengths were either ~435 nucleotides (half sequences) or ~856 nucleotides (whole sequences; Table 1). DNA sequence data were deposited at GenBank (Table 1).

Base frequencies and sequence variation and divergence values were calculated using MEGA 3.1 (Kumar et al. 2004). Trees were visualized with TreeView (Page 1996). Maximum likelihood (ML) analyses were performed using PAUP* 4.0b10 (Swofford 2002) with models meeting the Akaike information criterion in Modeltest 3.06 (Posada and Crandall 1998). Bootstrap analyses consisted of 10 heuristic searches with random addition of taxa and TBR branch swapping and reanalysis of the data 100 times. MrBayes 3.0 (Huelsenbeck and Ronquist 2001) was used to estimate

model parameters from the data and estimate the phylogeny with branch support values. Mixed models were used to build trees when cytb and βfib7 data were combined. Markov chains ran for 5 million generations. A shorter run of one million generations was used to assess stationarity (burn-in). Markov chains were sampled every 1,000 generations, yielding 5,000 point estimates of parameters. These subsamples, minus the burn-in generations, were used to create Bayesian consensus trees and to identify posterior probabilities for tree nodes.

RESULTS

Cytb of 27 individuals of eight *Progne* species and βfib7 of 20 individuals of six species were sequenced (Table 1). We failed to obtain cytb from museum specimens of *P. modesta* and βfib7 from museum specimens of *P. modesta*, *P. murphyi*, and *P. sinaloae*. Multiple individuals of most species were sequenced to examine intraspecific variation (Table 1). Cytb sequences of *P. sinaloae* and *P. murphyi* individuals were invariable; thus, we used only one sequence of each for phylogenetic reconstruction. Martin cytb varied at 160 nucleotide sites and was potentially informative at 114 sites. βfib7 varied at 26 sites and was potentially informative at 11 sites. Most cytb nucleotide substitutions occurred at third codon positions (81%), followed by first positions (17%) and second positions (3%). Amino acids varied at 17 sites and were potentially informative at nine sites. Cytb sequences appeared to be mitochondrial, not nuclear, because amino acid substitutions were similar in chemical properties, no stop codons occurred, and third position changes predominated. The mean (range) of nucleotide composition was: thymine 24.8 (23.8–26.6), cytosine 34.4 (33.1–35.2), adenine 27.0 (25.9–27.4), and guanine 13.8 (13.3–14.3). A relatively even distribution of bases occurred at first codon positions (T 23.8, C 29.1, A 23.3, G 23.7); less at second positions (T 41.0, C 26.7, A 19.6, G 12.7), and even less at third positions (T 9.5, C 47.6, A 38.1 G 4.8).

Cytb distances between *Progne tapera* and other *Progne* species averaged 7.6% (range: 6.7–8.3%). Distances among the seven species of *Progne* (sensu stricto) averaged 4.9% (0.1–6.9%). An unexpectedly large cytb distance occurred between Central American and Amazonian populations of *P. chalybea* (average 5.7%), and a remarkably short distance occurred between South American *P. chalybea* and *P. elegans* (0.8%). βfib7 distances between *P. tapera* and other *Progne* species averaged 1.8% (1.3–2.0%). Distances among five species of *Progne* (sensu stricto) averaged 0.4% (0–1.0%). The average distance between Central American and Amazonian populations of *P. chalybea* was 0.4%, between Amazonian *P. chalybea* and *P. elegans* 0.3%, and between *P. elegans* and Central American *P. chalybea* 0.2%. Only nine sites were variable and only four were potentially parsimony informative in comparisons of *P. chalybea* and *P. elegans*. None of the informative sites was synapomorphic for Central American and Amazonian populations of *P. chalybea* or for South American *P. chalybea* and *P. elegans*.

ML bootstrap and Bayesian analyses of cytb and combined cytb and βfib7 data yielded consistent trees. However, the combined tree provided less resolution than the cytb tree among closely related taxa (e.g., among *P. subis* subspecies), presumably because of the influence of slower evolving βfib7 sequences. We present the cytb tree as the optimal tree (Fig. 1), i.e., the tree that depicts basal relationships found in the combined tree and distal relationships provided by the fast-evolving cytb gene. All branches with less than 95% Bayesian or 87% bootstrap support in this tree can be collapsed. When this is done, unambiguous relationships are derived. *P. tapera* is sister to the rest of *Progne*. Three clades emerge among the other taxa. *P. subis* is monophyletic and divided into western *P. s. aboricola* and eastern *P. s. subis*. Included in the eastern clade is a wintering specimen collected in Brazil. The Middle American taxa form a clade. This group includes *P. cryptoleuca* and its sister taxon *P. dominicensis*, as well as *P. sinaloae* and *P. chalybea* from Costa Rica and Panama. *P. murphyi* is distinct from *P. elegans*. The latter forms a clade with South American populations of *P. chalybea*, making that taxon polyphyletic.

DISCUSSION

We assumed at the outset that species of *Progne* would be substantially diverged from one another and, thus, appropriate for phylo-

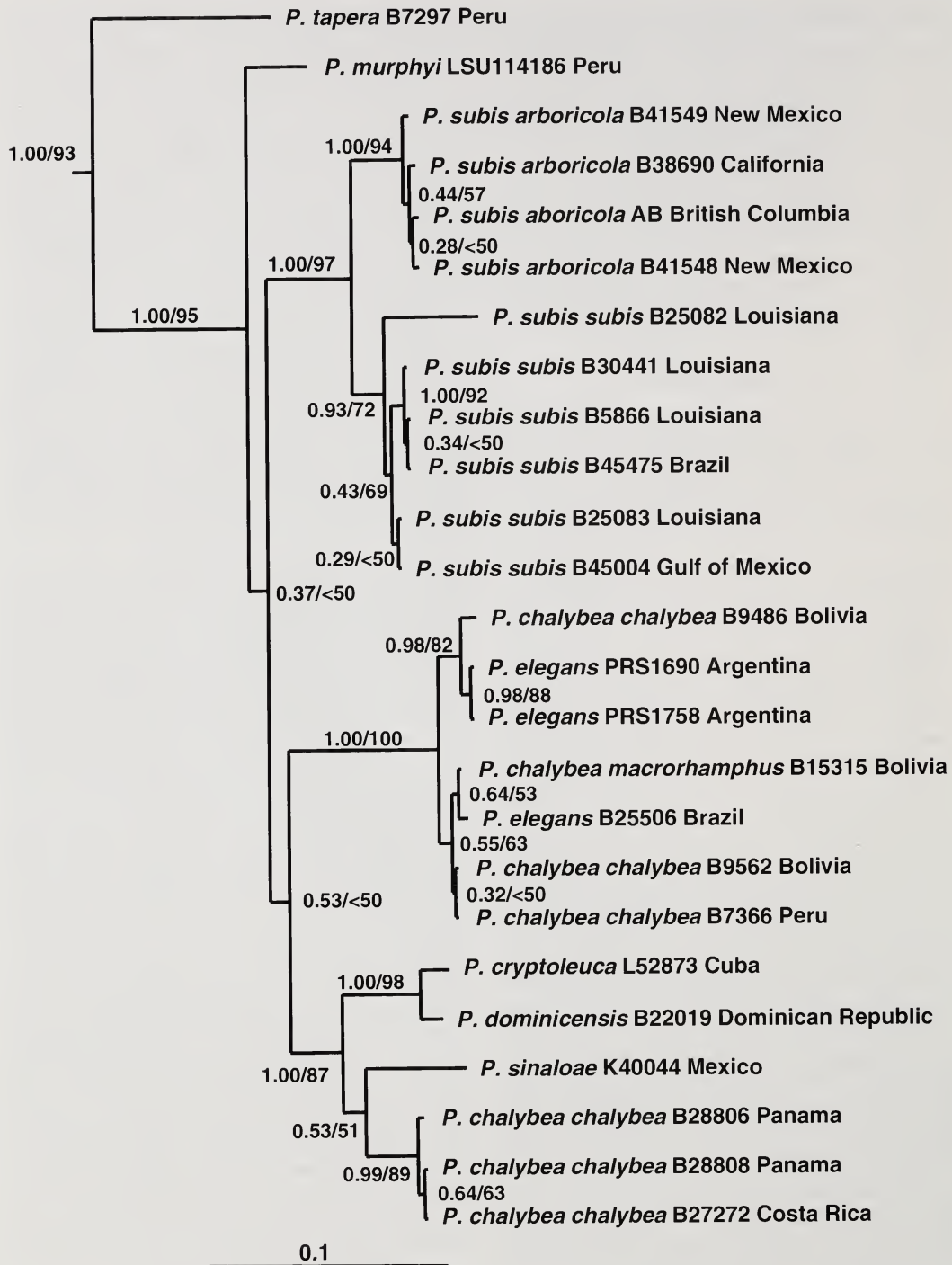


FIG. 1. Estimate of *Progne* phylogeny from cytb data. Numbers on branches are Bayesian/ML bootstrap support. The ML model is GTR + I + G; −lnL = 4020.2771; base frequencies: A = 0.30, C = 0.37, G = 0.11, T = 0.22; rate matrix: A–C = 16.9964, A–G = 248.2475, A–T = 23.0512, C–G = 6.0181, C–T = 101.1734, G–T = 1.0000; proportion of invariable sites = 0.52; and gamma distribution shape parameter = 0.64.

genetic study. Our comparisons, however, indicate remarkably close relationships between some species (e.g., *P. dominicensis* and *P. cryptoleuca*) and polyphyly and possibly hybrid introgression in others (*P. chalybea* and *P. elegans*). These results suggest that ultimate understanding of relationships among some *Progne* taxa will require a population genetic rather than a phylogenetic perspective. Unfortunately, *Progne* tissues are poorly represented in museum collections and we have not been able to sample the group adequately for a thorough analysis. However, our study provides insight into *Progne* phylogeny on several levels. It illuminates relationships among *P. subis* populations in the USA and Canada, largely supports the current nine species classification, and provides evidence of higher level relationships among some species in the genus, particularly those in Middle America.

The phylogenetic analysis strongly supports the traditional division of New World martins into two groups (Fig. 1): *P. tapera* versus all other species (*Progne* sensu stricto). We suggest that *P. tapera* remain in *Progne* as currently classified rather than in the monotypic genus *Phaeoprogne*. The current arrangement emphasizes its close relationship to the rest of the New World martin species as opposed to other groups of swallows (Sheldon and Winkler 1993, Sheldon et al. 2005).

The taxonomically difficult part of the genus, *Progne* sensu stricto, remains partially unresolved, but three well supported clades are evident (Fig. 1).

(1) *Progne subis* of North America forms a distinct group. It is diverged by an average cytb distance of 5.6% from all other *Progne* species (sensu stricto) and is not particularly close to Middle American species. There is a clear division within *P. subis* between eastern and western subspecies, *subis* and *arboricola*. This division coincides with a boundary at the Rocky Mountains previously recognized based on morphological and life history differences. Birds from northern Arizona, Utah, northern Rockies, and the Pacific Northwest are generally larger than eastern birds, and females of western birds have whiter underparts and foreheads than their eastern counterparts (Brown 1997). Subspecific division of western populations, particularly those in the northern Rockies and northern Pacific coast, has been uncertain (Brown 1997). Our data indicate a close genetic relationship between populations in British Columbia and those in southwestern New Mexico and southern California. Thus, these populations are appropriately classified as a single taxonomic group. Both *subis* and *arboricola* in northern Mexico are thought to occur in highland areas (Phillips 1986, Brown 1997), but we had no material from that region for comparison. We also lacked samples of the third subspecies, *hesperia*. This lowland taxon occurs in deserts of southern Baja California, Sonora, and along the coast of Mexico to northern Sinaloa. It is well known for nesting in cacti.

(2) Martins in Middle America form a clade consisting of *Progne dominicensis*, *P. cryptoleuca*, *P. sinaloae*, and Central American *P. chalybea*. A close relationship among these taxa has long been suspected (Eisenmann 1959, Phillips 1986, Sibley and Monroe 1990). The cytb of *P. dominicensis* and *P. cryptoleuca* is diverged by only 1.2%, and these two taxa form a monophyletic group. They may be considered different species because of their allopatry and reduced white on the belly of male *P. cryptoleuca* (McKitrick and Zink 1988), or they may be considered conspecific given their monophyly and genetic and plumage similarities (Johnson et al. 1999). *P. sinaloae* cytb is 3.5% diverged from that of Caribbean taxa and 3.4% diverged from that of *P. chalybea*. *P. sinaloae* appears to be a distinct species despite similarities in plumage to *P. dominicensis*, *P. cryptoleuca*, and *P. chalybea* (Zimmer 1955, Eisenmann 1959).

(3) The southern martins appear not to be conspecific. *P. murphyi* of northwestern Peru is distinct from *P. elegans*, which occurs east of the Andes. *P. murphyi* is smaller, has less white in the female plumage, and differs from *P. elegans* in cytb sequence by 5.6%. We found that *P. elegans* is unexpectedly close to southern populations of *P. chalybea* (0.8% cytb divergence). *P. chalybea*, in turn, appears to be polyphyletic. Its Amazonian populations are close to *P. elegans*, whereas its Central American populations form a clade with Middle American taxa (average cytb divergence 3.5%). Not only is cytb of Amazonian *P. chalybea* substantially different from that of Cen-

tral American populations (5.7% divergence), but individuals from central Amazonia are darker-throated and males have a larger amount of blue on the sides of their breasts than individuals from trans-Andean and Central American populations (D. F. Lane, pers. comm.). Both cis- and trans-Andean *P. chalybea* are classified as the same subspecies (*chalybea*) despite these differences. The other subspecies, *macrorhamphus* from southeastern Amazonia, is strikingly pale-throated compared to *chalybea* of central Amazonia, but the genetic difference between these groups is negligible (0.1% cytb divergence).

It is conceivable that Amazonian populations of *P. chalybea* represent an unrecognized taxon that is closely related to *P. elegans*. This seems unlikely, however, because of consistent plumage differences between *P. chalybea*, which is steel-blue above and extensively pale below, and *P. elegans*, whose males are all blue. Another explanation is interspecific hybridization between the two species. Hybridization is known to occur (Eisenmann and Haverschmidt 1970, Short 1975) and may have resulted in introgression of *P. elegans* mtDNA into Amazonian *P. chalybea*. Introgression would explain why the mtDNA of Amazonian and Central American *P. chalybea* is so different. Unfortunately, nuclear βfib7 data do not support or refute this idea. *P. elegans* and the Central and South American populations of *P. chalybea* have similar βfib7 sequences (0.2–0.4% divergence), and no nucleotide substitutions are synapomorphic for any pair of populations.

Future work on the evolution and biogeography of New World martins will require improved sampling. The position of the Galapagos Martin (*P. modesta*) remains in doubt. It is usually considered to be closely related to *P. murphyi* and *P. elegans* based on plumage, but this arrangement seems unlikely given the genetic distinctness of *P. murphyi* and *P. elegans* from one another. A more likely explanation is that Galapagos Martin derives from errant migrant populations. The problem of polyphyly in *P. chalybea* needs to be approached with greater sampling from northern South America to help gauge genetic variation across the entire range of the species. Several other relationships within *Progne* also merit examination, for example, the connection of the three subspecies of *P. subis* in Mexico and the genetic distinctiveness of *P. chalybea warneri* in western Mexico.

ACKNOWLEDGMENTS

We thank A. J. Baker, E. A. Cardiff, S. W. Cardiff, Mario Cohn-Haft, D. L. Dittmann, N. K. Klein, M. B. Robbins, R. S. Ridgely, F. Sornoza Molina, Paul Sweet, Katherine Wallace, Bret Whitney, Academy of Natural Sciences of Philadelphia, American Museum of Natural History, Cornell University, LSU Museum of Natural Science, Museum of Vertebrate Zoology, University of Kansas Natural History Museum, Royal Ontario Museum, and Smithsonian Institution for help obtaining tissues. Daniel F. Lane provided advice on plumage variation in Gray-breasted Martin. We also thank the Museo Ecuatoriano de Ciencias Naturales and the Ministerio de Agricultura, Quito; and institutions in Bolivia, Dominican Republic, Ecuador, Mexico, Panama, and Peru for their roles in making specimens and tissues available for study. This research was supported financially by the American Museum of Natural History, LSU Museum of Natural Science, Museum of Vertebrate Zoology, National Zoo, and NSF/LaSER 1993-96-ADP-02.

LITERATURE CITED

American Ornithologists' Union (AOU). 1998. Check-list of North American birds. Seventh Edition. American Ornithologists' Union, Washington, D.C., USA.

Avise, J. C., W. S. Nelson, and C. G. Sibley. 1994. DNA sequence support for a close phylogenetic relationship between some storks and New World vultures. Proceedings of the National Academy of Science of the USA 91:5173–5177.

Brown, C. R. 1997. Purple Martin (*Progne subis*). The birds of North America. Number 287.

Desjardins, P. and R. Morais. 1990. Sequence and gene organization of the chicken mitochondrial genome, a novel gene order in higher vertebrates. Journal of Molecular Biology 212:599–634.

Dickinson, E. C. 2003. The Howard & Moore complete checklist of the birds of the world. Third Edition. Christopher Helm, London, United Kingdom.

Eisenmann, E. 1959. South American migrant swallows of the genus *Progne* in Panama and northern South America; with comments on their identification and molt. Auk 76:528–532.

Eisenmann, E. and F. Haverschmidt. 1970. Northward migration to Surinam of South American martins (*Progne*). Condor 72:368–369.

Hellmayr, C. E. 1935. Catalogue of the birds of the Americas. Part 8. Field Museum of Natural History Zoological Series 13:1–541.

Helm-Bychowski, K. and J. Cracraft. 1993. Recovering phylogenetic signal from DNA sequences: relationships within the corvine assemblage (class Aves) as inferred from complete sequences of the

mitochondrial DNA cytochrome-*b* gene. Molecular Biology and Evolution 10:1196–1214.

Hillis, D. M., A. Larson, S. K. Davis, and E. A. Zimmer. 1990. Nucleic acids. III. Sequencing. Pages 318–370 *in* Molecular systematics (D. M. Hillis and C. Moritz, Editors). Sinauer Associates, Sunderland, Massachusetts, USA.

Huelsenbeck, J. P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

Johnson, N. K., J. V. Remsen, and C. Cicero. 1999. Resolution of the debate over species concepts in ornithology: a new comprehensive biologic species concept. Proceedings of the International Ornithological Congress 22:1470–1482.

Kocher, T. D., W. K. Thomas, A. Meyer, S. V. Edwards, S. Paabo, F. X. Villablanca, and A. C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences of the USA 86: 6196–200.

Kumar, S., K. Tamura, and M. Nei. 2004. MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. Briefings in Bioinformatics 5:150–163.

McKitrick, M. C. and R. M. Zink. 1988. Species concepts in ornithology. Condor 90:1–14.

Page, R. D. M. 1996. TREEVIEW: an application to display phylogenetic trees on personal computers. Computer Applications in the Biosciences 12: 357–358.

Peters, J. L. 1960. Family Hirundinidae. Pages 80–129 *in* Check-list of birds of the world. Volume 9 (J. L. Peters, Editor). Museum of Comparative Zoology, Cambridge, Massachusetts, USA.

Phillips, A. R. 1986. The known birds of North and Middle America. Part I. Allan R. Phillips, Denver, Colorado, USA.

Posada, D. and K. A. Crandall. 1998. ModelTest: testing the model of DNA substitution. Bioinformatics 14:817–818.

Prychitko, T. M. and W. S. Moore. 1997. The utility of DNA sequences of an intron from the beta-fibrinogen gene in phylogenetic analysis of woodpeckers (Aves: Picidae). Molecular Phylogenetics and Evolution 8:193–204.

Sheldon, F. H. and D. W. Winkler. 1993. Intergeneric phylogenetic relationships of swallows estimated by DNA-DNA hybridization. Auk 110:798–824.

Sheldon, F. H., L. A. Whittingham, R. G. Moyle, B. Slikas, and D. W. Winkler. 2005. Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 35:254–270.

Short, L. L. 1975. A zoogeographic analysis of the South American Chaco avifauna. Bulletin of the American Museum of Natural History 154:165–352.

Sibley, C. G. and B. L. Monroe. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, USA.

Slikas, B., I. Jones, S. Derrickson, and R. Fleischer. 2000. Phylogenetic relationships of Micronesian white-eyes based on mitochondrial sequence data. Auk 117:355–365.

Swofford, D. L. 2002. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts, USA.

Turner, A. K. 2004. Family Hirundinidae (swallows and martins). Pages 602–685 *in* Handbook of the birds of the world. Volume 9 (J. del Hoyo, A. Elliott, and D. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Whittingham, L. A., B. Slikas, D. W. Winkler, and F. H. Sheldon. 2002. Phylogeny of the Tree Swallow genus (Aves: *Tachycineta*) by Bayesian analysis of mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 22:430–441.

Zimmer, J. T. 1955. Studies of Peruvian birds. Number 66. The swallows (Hirundinidae). American Museum Novitates 1723:1–35.

The Wilson Journal of Ornithology 120(4):692–699, 2008

PRELIMINARY ANALYSIS OF THE ECOLOGY AND GEOGRAPHY OF THE ASIAN NUTHATCHES (AVES: SITTIDAE)

SHAILY MENON,[1,5] ZAFAR-UL ISLAM,[2,4] JORGE SOBERÓN,[3] AND A. TOWNSEND PETERSON[3]

ABSTRACT.—We explored distributions of Asian nuthatch species in ecological and geographic space using ecological niche modeling based on occurrence data associated with specimens and observations. Nuthatches represent a well-defined clade occurring throughout the Northern Hemisphere, but are most diverse in southern Asia where 15 of the 24 species occur and where the lineage is believed to have evolved. Species richness was focused in a narrow east–west band corresponding to the forested parts of the Himalayas with a maximum number of nine species predicted present in these foci. The distributional predictions have a mid-elevation focus with highest species diversity between 1,000 and 2,000 m. Niche breadth and volume were positively related, but accumulation of distributional area (niche volume) decreased with additional environmental combinations (niche breadth). The extent of potential range filling, a measure of distributional disequilibrium, was connected with montane habit (R^2 = 0.422) indicating that montane situations limit the distributional potential of species. *Received 13 September 2007. Accepted 1 February 2008.*

The Sittidae consists of 25 species in two genera: *Sitta* with 24 species (nuthatches) and *Tichodroma* with a single species (Wallcreeper [*T. muraria*]). The family was conceived much more broadly (Mayr and Amadon 1951) to contain other, superficially similar groups, such as *Daphoenositta* (the sittellas of New Guinea and Australia), now known to have converged on a similar feeding niche and morphology from different ancestry (Sibley and Ahlquist 1990). True nuthatches occur throughout the Northern Hemisphere, but are most diverse in southern Asia where 15 of the 24 species occur (Harrap and Quinn 1995), and where the lineage probably evolved (Matthysen 1998). The co-occurrence of many closely-related species was noted by Ripley (1959) and Lack (1971). Matthysen (1998) observed that many nuthatch species have small ranges, although 5–7 nuthatch species occur at sites across southeast Asia, generally segregated by elevation, habitat, or both (Lack 1971, Matthyssen 1998).

Nuthatch distributions range from narrow endemism to broad distributions crossing continents. For example, the White-browed Nuthatch (*Sitta victoriae*) is microendemic, restricted to Mount Victoria in western Burma; in contrast, Eurasian Nuthatch (*S. europaea*) ranges across much of Eurasia. Nuthatches are typical in temperate and subtropical areas of the Northern Hemisphere with two species (*S. europaea* and *S. canadensis*) occurring well into the subarctic, almost to the northern edge of the boreal forest (Matthysen 1998). Fewer nuthatch species occur in tropical regions of southern Asia and only two (*S. frontalis* and *S. azurea*) reach the Equator.

New informatic approaches offer novel insights into the interaction between ecology and geography in evolving lineages (Soberón and Peterson 2004, 2005). In particular, diverse hypotheses relevant to distributional ecology and biogeography can be tested: conservatism of ecological niche characteristics (Peterson et al. 1999), ecological innovation (Peterson and Holt 2003, Graham et al. 2004), distributional equilibrium with climate features (Svenning and Skov 2004), identification of barriers to dispersal (Peterson 2003), the role of interspecific competition in shaping species' distributions (Anderson et al. 2002), and others. The objective of this paper is to analyze and explore the ecology and distributions of Asian nuthatch species as a first step toward a more integrative view of nuthatch evolution and biogeography.

METHODS

Data.—We focused on 14 species in the genus *Sitta* and one species in the genus *Ti-*

[1] Biology Department, Grand Valley State University, Allendale, MI 49401, USA.

[2] Bombay Natural History Society, Mumbai, India.

[3] Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, KS 66045, USA.

[4] Current address: National Wildlife Research Center, Taif, Saudi Arabia.

[5] Corresponding author; e-mail: menons@gvsu.edu

TABLE 1. Species analyzed and occurrence data available for each. Crude estimates of actual distribution area, potential distribution area, and proportional range filling are included.

Species	Common name	Number of occurrence points	Actual distribution area (km^2)	Potential distribution area (km^2)	Proportional range filling
Sitta cashmirensis	Kashmir Nuthatch	17	5,387	21,739	0.25
S. castanea	Chestnut-bellied Nuthatch	69	44,362	98,433	0.45
S. europaea	Eurasian Nuthatch	40	240,678	275,212	0.87
S. formosa	Beautiful Nuthatch	63	7,800	24,618	0.32
S. frontalis	Velvet-fronted Nuthatch	60	41,620	83,444	0.5
S. himalayensis	White-tailed Nuthatch	27	5,829	93,258	0.06
S. leucopsis	White-cheeked Nuthatch	23	10,212	38,181	0.27
S. magna	Giant Nuthatch	45	7,448	18,345	0.41
S. nagaensis	Chestnut-vented Nuthatch	27	9,512	41,953	0.23
S. solangiae	Yellow-billed Nuthatch	3	77	2,171	0.04
S. tephronota	Eastern Rock Nuthatch	34	29,776	71,930	0.41
S. victoriae	White-browed Nuthatch	2	48	48	1.00
S. villosa	Chinese Nuthatch	10	11,779	46,344	0.25
S. yunnanensis	Yunnan Nuthatch	7	3,005	11,830	0.25
Tichodroma muraria	Wallcreeper	56	126,802	142,392	0.89

chodroma occurring in Eurasia. Occurrence information was accumulated from natural history museums across North America, including the Museum of Comparative Zoology, Field Museum of Natural History, University of Kansas Natural History Museum, and the U.S. National Museum of Natural History; data were also drawn from data bases developed by BirdLife International (Collar et al. 2001). Textual descriptions of occurrence localities were translated into geographic coordinates in decimal degrees using the GeoNet Names Server (National Geospatial Intelligence Agency 2007) and BioGeomancer (Chapman and Wieczorek 2006). The final data set consisted of 483 occurrence points with samples for individual species ranging from 2 to 69 (Table 1). The amount of occurrence data available for Asian nuthatch species was variable. For most species, we had more than sufficient information to characterize ecology and distribution. However, in two or three cases, sample sizes available were marginal (*Sitta victoriae*, 2 points; *S. solangiae*, 3 points; *S. yunnanensis*, 7 points). Some analyses suggest these sample sizes are probably too low (Stockwell and Peterson 2002b), but others indicate that such models may be viable (Peterson et al. 2006). These three species are genuinely microendemics and a few points are likely to be most of what is available, particularly in the single mountain range endemic *S. victoriae*. Our analyses do not involve any projections to other time periods or other regions; we believe the effects of the potentially poor fit of these models are slight.

Climate data (1960–1990) were drawn from the WorldClim climate data archive (Hijmans et al. 2005). We used a subset of the 'bioclimatic' coverages: annual mean temperature, mean diurnal temperature range, maximum temperature of warmest month, minimum temperature of coldest month, annual total precipitation, and precipitation of wettest and driest months. We supplemented these data sets with information from the U.S. Department of Interior, Geological Survey's Hydro-1K data set (USDI 2001) for topography and landform (slope, aspect, compound topographic index). We resampled all data sets to 0.17° resolution to avoid over interpretation of the precision of the point-occurrence data.

Ecological Niche Modeling.—We used ecological niche modeling to provide a picture of likely distributional patterns for each species. This general class of procedures is based on known occurrences of species, as they relate to digital raster data coverages that summarize potentially relevant ecological parameters. The goal is to identify a suite of ecological conditions within which the species in question can likely maintain populations without immigration subsidy (Grinnell 1917). The result is a picture of the species' potential geographic distribution, defined as the area meeting the species' ecological niche requirements

that characterize known distributional areas (Soberón and Peterson 2005). We used the Genetic Algorithm for Rule-set Prediction, or GARP (Stockwell and Peters 1999), which has seen extensive testing and application to such questions (Peterson and Cohoon 1999; Stockwell and Peterson 2003; Stockwell and Peterson 2002a, 2002b). GARP is an evolutionary-computing approach that relates known occurrences of species to raster data layers summarizing relevant environmental parameters to create a model of the ecological niche of the species, which can be used to identify a potential geographic distribution (Soberón and Peterson 2005). We used 19 bioclimatic variables from the WorldClim global 0.17° data set (Hijmans et al. 2005), plus data on topography and landform including elevation, slope, aspect, and compound topographic index (USDI 2001) to characterize ecological landscapes.

Our use of GARP is for visualization and interpolation purposes only, and the technique has been documented in detail elsewhere (Anderson et al. 2002, 2003; Illoldi et al. 2004; Martínez-Meyer et al. 2004; Ortega-Huerta and Peterson 2004; Soberón and Peterson 2004; Peterson 2005). Thus, we do not provide a full, detailed description. We used half of the available occurrence data for training models, and half to provide test data sets that characterized model success in predicting independent occurrence points. We developed 100 replicate models for each species using GARP and followed recent recommended protocols (Anderson et al. 2003) in using independent measures of omission and commission (Type I and Type II) prediction error to identify an optimal 10% of models from the 100 replicate models originally produced. The sum of these 10 models was taken as the best hypothesis of the species' distribution.

We inspected the distributional hypotheses for each species to establish a threshold for decisions of presence versus absence (lowest training presence threshold, Pearson et al. 2007). Initial model predictions in two cases (*S. yunnanensis* and *S. nagaensis*) were too broad and general and we used a tighter convergence criterion (convergence 0.001; maximum iterations 10,000), which resulted in closer correspondence between model predictions and known distributional limits. No tests of model quality were developed given uneven sample sizes across species and known ability of Ecological Niche Models (ENMs) to reconstruct the generalities of species' distributions at continental scales (Elith et al. 2006).

We related model predictions for each species to the original ecological variables on which the models were based to reconstruct models in ecological space. We used the 'Grid Combine' option in ArcGIS 9.0 to create a grid with a distinct value for all unique combinations of the environmental coverages across Eurasia. The attributes table associated with this grid yielded a matrix showing all unique environmental combinations and predictions associated with each species, which permitted several visualization exercises. Niche breadth was reconstructed as the variance of distributions in a standardized principal components analysis (Rotenberry and Wiens 1980, Carnes and Slade 1982, Litvak and Hansell 1990). Niche volume was calculated as the spatial translation of the niche in terms of areal coverage of the distribution across the landscape of interest without attention to which part is actually occupied by the species (Soberón 2007).

We established which portions of the potential distributional area are likely not to be inhabited to explore differences between actual and potential distributional areas (Svenning and Skov 2004). We were conservative and only eliminated as uninhabited those areas that were disjunct from areas of known occurrence, and from which no occurrences were known. These steps resulted in maps of the likely actual area of occurrence (Soberón and Peterson 2005). Proportional range occupancy was calculated as the ratio of the areas covered by the actual and potential distributional areas. We classed each species as occurring primarily in lowlands, foothills, or at high elevations based on published descriptions of nuthatch natural history (Matthysen 1998).

RESULTS

Niche Models.—These models produced realistic predicted distributions. For example, we used 17 available unique occurrence points for *S. cashmirensis* to characterize the species' distribution (Fig. 1). Initial results from the

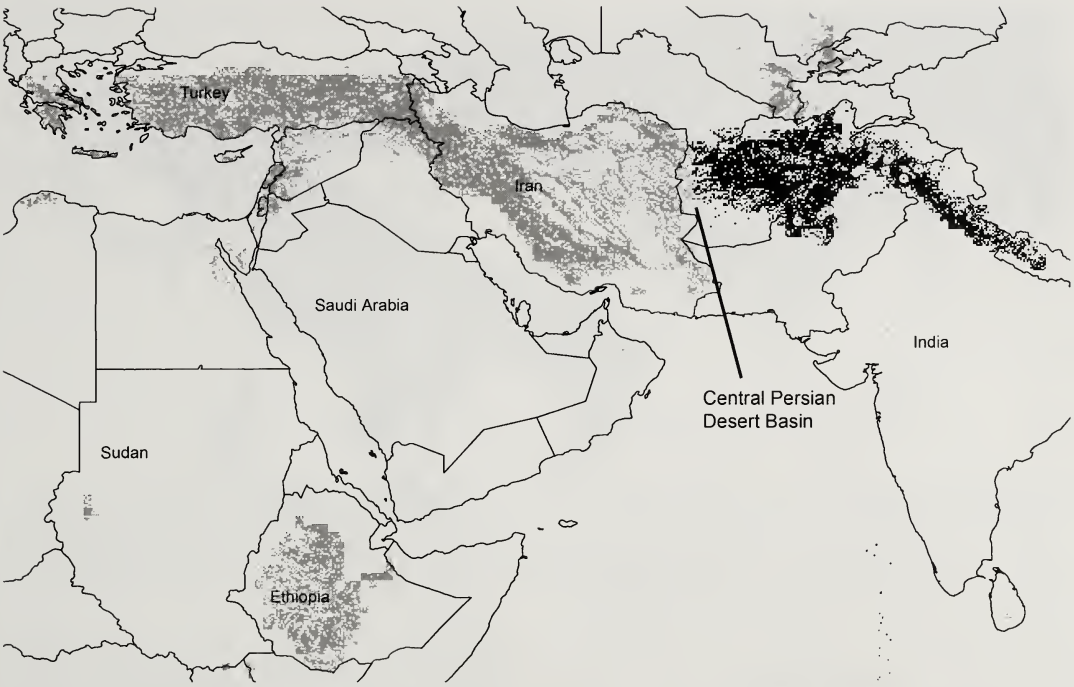


FIG. 1. Kashmir Nuthatch (*Sitta cashmirensis*) illustrating known occurrence points (dotted circles), crude potential geographic distribution (gray shading), and estimated actual distribution (black shading).

ENM algorithm identified mainly highland areas as potential distributional areas including the Himalayas of India, Nepal, and Pakistan (that constitute the known range of the species), as well as the highlands of Ethiopia and lower-elevation regions of Iran, Turkey, and Greece. A major disjunction in this distributional prediction corresponds to the dispersal barrier likely constraining this species to its present distribution: the Central Persian Desert Basin in central and eastern Iran, and western Afghanistan.

Geographic patterns of species richness based on the modeled distributions of nuthatch species were striking (Fig. 2). Spread generally across southern Asia, nuthatches show a dramatic richness focus in a narrow east-west band corresponding to the forested parts of the Himalayas, extending eastward into southwestern China (especially Szechuan and Yunnan provinces) and northern Burma. These foci reach predicted species richness up to nine species present (Fig. 2). However, the coarse resolution of our predictions (0.17°, or ~18.9 km) precludes separation of local species richness from high local-scale species turnover corresponding to local habitat diversity. These distributional predictions have a middle elevation focus (Fig. 3) with lowland areas and elevations above ~3,000 m having relatively few species; intervening elevations (1,000–2,000 m), have the highest species diversity.

Niche Dimensions and Disequilibrium.— The relationship between niche breadth and extent was positive (Fig. 4) because wide niche breadths tend to map onto large geographic areas, but accumulation of distributional area (niche volume) decreases with additional environmental combinations (niche breadth). Proportional range-filling indices showed a negative relationship with montane habit (Fig. 5). An outlier in this relationship was the White-browed Nuthatch; regressions including this species explained 10% of the overall variation ($R^2 = 0.102$; $P < 0.05$), whereas excluding it explained fourfold more variation ($R^2 = 0.422$; $P < 0.05$). The probable relictual nature of this species needs further investigation, but montane characteristics clearly limit the distributional potential of nuthatch species.

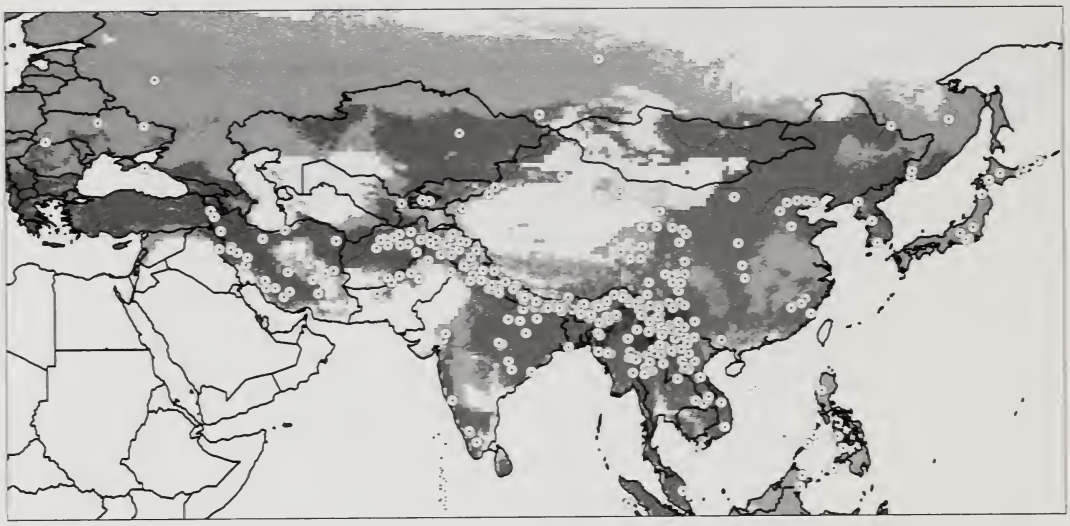


FIG. 2. Overall patterns of predicted species richness among Asian nuthatches (ramp from white = 0 species predicted present, darkest gray = 9 species predicted present). Sampling points (i.e., occurrence records for the 15 species in the study) are shown as dotted circles.

DISCUSSION

Niche breadth and volume represent two measures of the ecological niche amplitude of a species, the former in terms of ecological combinations and the latter reflecting the spatial manifestation (Soberón 2007). These quantities are only beginning to be characterized and few studies have explored their relationships. The positive niche breadth and volume relationship observed in this study is of interest and should be explored in additional groups.

Recent studies have explored the extent to which species fill their potential distributions, a measure of distributional disequilibrium (Svenning and Skov 2004). We generally found low proportional range filling among nuthatch species, particularly those with montane distributions. This suggests that nuthatch distributions will frequently be constrained by limited dispersal abilities.

Montane Ecology and Geography.—Nuthatch diversity patterns are related to the major mountain systems and associated cool tem-

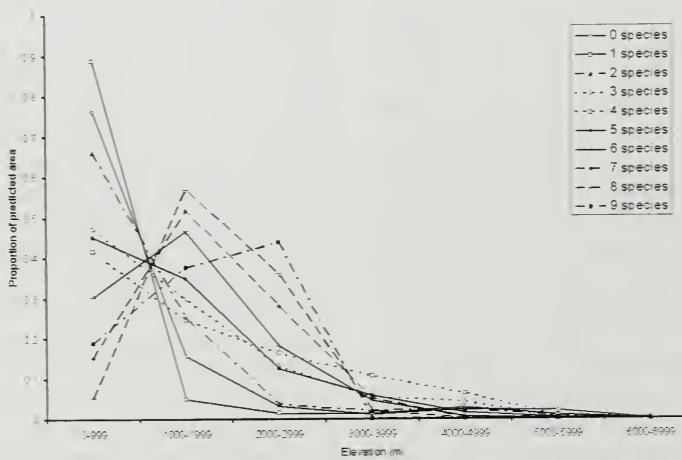


FIG. 3. Relationship between number of nuthatch species predicted present and elevation across Asia.

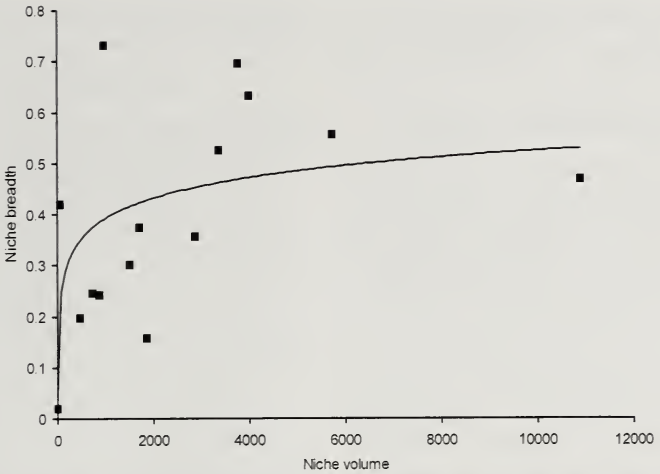


FIG. 4. Relationship between niche volume and niche breadth. Niche breadth is measured as the average variance across the uncorrelated principal components, whereas niche volume is the geographic projection (in km^2) of the ecological niche model.

perate climates. Most nuthatch species have narrow geographic distributions in subtropical regions; those few with broader distributions range considerably farther and more broadly. The nuthatch diversity focus coincides closely with the Qinghai-Tibet Plateau region known to contain the largest concentration of Endemic Bird Areas in Asia (Long et al. 1996), as well as a focus of bird species richness (Ding et al. 2006). This association illustrates the seeming contradiction that most nuthatch species have small ranges, but the temperate-zone conditions they prefer are represented much more broadly farther to the north.

These results raise issues of biogeography and the role of geography in subdividing geographic distributions of evolving lineages. If species do not fill their ranges as completely in montane environments as in lowland environments, and if ecological niches are relatively conservative (Peterson et al. 1999), interactions may exist between geographic potential and ecological habit. Lowland species may have broader geographic distributions, but montane species may experience greater subdivision or have greater potential for isolation of populations that manage to colonize across dispersal barriers. Tests of these and

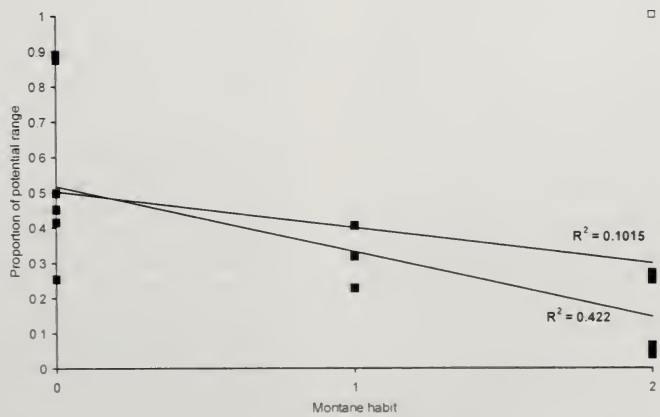


FIG. 5. Relationship between proportion of potential distribution actually occupied and montane habit (0 = lowlands, 1 = foothills, 2 = high elevations). Shown are two simple linear regressions, one including (R^2 = 0.102) and the other excluding (R^2 = 0.422) *Sitta victoriae* (open box).

other hypotheses will be feasible once a robust phylogenetic hypothesis is available for the group.

CONSERVATION IMPLICATIONS

One fifth of all Asian nuthatch species are considered threatened (Collar et al. 1994, IUCN 2006). Among threatened Asian species, *S. victoriae* has an extremely narrow range, is listed as Endangered (IUCN 2006), and would clearly be threatened by any significant habitat destruction in the Mount Victoria region. Four other species (*S. solangiae*, *S. yunnanensis*, *S. formosa*, *S. magna*) have wider ranges, but are threatened by habitat loss and degradation (Matthysen 1998, BirdLife International 2004, IUCN 2006). *Sitta formosa* and *S. magna* have small populations, which are thought to be declining and severely fragmented, and are listed as Vulnerable. *Sitta solangiae* and *S. yunnanensis* are affected by ongoing habitat loss and degradation, but have larger populations and are listed as near Threatened (IUCN 2006). The area of highest nuthatch species diversity, predicted by our analysis, closely matches the Sino-Himalayan Mountain Forest region identified by BirdLife International (2003) as one of nine key forest regions for threatened birds in Asia.

The Chinese and Himalayan region consists of middle- and high-elevation forests, scrub, and grasslands on the southern slopes of the Himalayas and in the mountains of southwestern China and northern Indochina. The natural habitat in this region is relatively secure at higher altitudes compared to middle elevations, which is under greater pressure from deforestation and fragmentation. Middle-elevation forests are also the areas where our analysis predicts highest nuthatch species diversity. Habitat fragmentation further compounds the conservation implications for montane species, which have a greater potential for isolation. Our results emphasize the importance of middle-elevation habitats in this region for biodiversity.

ACKNOWLEDGMENTS

This research was supported by an NSF-Research Opportunity Award. We gratefully acknowledge Asad Rahmani (Director, Bombay Natural History Society) for support, Monica Papeş for technical assistance, and Jill Witt for introducing the Beautiful Nuthatch (*Sitta formosa*) to the Menon Laboratory.

LITERATURE CITED

Anderson, R. P., D. Lew, and A. T. Peterson. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling 162:211–232.

Anderson, R. P., A. T. Peterson, and M. Gómez-Laverde. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos 93:3–16.

Birdlife International. 2003. Saving Asia's threatened birds: a guide for government and civil society. Birdlife International, Cambridge, United Kingdom.

Birdlife International. 2004. Threatened birds of the world 2004. CD-ROM. BirdLife International, Cambridge, United Kingdom.

Carnes, B. and N. Slade. 1982. Some comments on niche in canonical space. Ecology 63:888–893.

Chapman, A. D. and J. Wieczorek (Editors). 2006. Guide to best practices for georeferencing. Global Biodiversity Information Facility, Copenhagen, Denmark. www.gbif.org/prog/digit/data_quality/BioGeomancerGuide.pdf (accessed 10 August 2007).

Collar, N. J., M. J. Crosby, and A. J. Stattersfield. 1994. Birds to watch, 2. The world list of threatened birds. BirdLife Conservation Series Number 4. BirdLife International, Cambridge, United Kingdom.

Collar, N. J., A. V. Andreev, S. Chan, M. J. Crosby, S. Subramanya, and J. A. Tobias. 2001. Threatened birds of Asia: the BirdLife International Red Data Book. BirdLife International, Cambridge, United Kingdom.

Ding, T., H. Yuan, S. Geng, C. Koh, and P. Lee. 2006. Macro-scale bird species richness patterns of the East Asian mainland and islands: energy, area and isolation. Journal of Biogeography 33:683–693.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettman, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. E. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and A. T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology and Evolution 19:497–503.

Grinnell, J. 1917. Field tests of theories concerning distributional control. American Naturalist 51: 115–128.

Harrap, S. and D. Quinn. 1995. Chickadees, tits, nuthatches and treecreepers. Princeton University Press, Princeton, New Jersey, USA.

Hijmans, R. J., S. Cameron, and J. Parra. 2005. WorldClim. Version 1.3. University of California, Berkeley, USA. http://biogeo.berkeley.edu/worldclim/worldclim.htm (accessed 10 August 2007).

Illoldi, P., V. Sánchez-Cordero, and A. T. Peterson. 2004. Predicting distributions of Mexican mammals using ecological niche modeling. Journal of Mammalogy 85:658–662.

IUCN 2006. 2006 IUCN Red List of threatened species. http://www.iucnredlist.org (accessed 10 August 2007).

Lack, D. 1971. Ecological isolation in birds. Harvard University Press, Cambridge, Massachusetts, USA.

Litvak, M. and R. I. Hansell. 1990. A community perspective on the multidimensional niche. Journal of Animal Ecology 59:931–940.

Long, A. J., M. J. Crosby, and A. J. Sattersfield. 1996. Towards a global map of biodiversity: patterns in the distribution of restricted-range birds. Global Ecology and Biogeography Letters 5:281–304.

Martínez-Meyer, E., A. T. Peterson, and W. W. Hargrove. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13:305–314.

Matthysen, E. 1998. The nuthatches. T. and A. D. Poyser, London, United Kingdom.

Mayr, E. and D. Amadon. 1951. A classification of recent birds. American Museum Novitates 1946: 453–473.

National Geospatial Intelligence Agency. 2007. GEOnet Names Server (GNS). http://earth-info.nga.mil/gns/html/index.html (accessed 10 August 2007).

Ortega-Huerta, M. A. and A. T. Peterson. 2004. Modeling spatial patterns of biodiversity in northeastern Mexico. Diversity and Distributions 10: 39–54.

Pearson, R. G., C. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species' distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102–117.

Peterson, A. T. 2003. Predicting the geography of species' invasions via ecological niche modeling. Quarterly Review of Biology 78:419–433.

Peterson, A. T. 2005. Kansas Gap Analysis: the importance of validating distributional models before using them. Southwestern Naturalist 50:230–236.

Peterson, A. T. and K. C. Cohoon. 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. Ecological Modelling 117:159–164.

Peterson, A. T. and R. D. Holt. 2003. Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation. Ecology Letters 6:774–782.

Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Peterson, A. T., R. R. Lash, D. S. Carroll, and K. M. Johnson. 2006. Geographic potential for outbreaks of Marburg hemorrhagic fever. American Journal of Tropical Medicine and Hygiene 75:9–15.

Ripley, S. D. 1959. Character displacement in Indian nuthatches (*Sitta*). Postilla 42:1–11.

Rotenberry, J. T. and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

Sibley, C. G. and J. E. Ahlquist. 1990. Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven, Connecticut, USA.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10:1115–1123.

Soberón, J. and A. T. Peterson. 2004. Biodiversity informatics: managing and applying primary biodiversity data. Philosophical Transactions of the Royal Society of London, Series B 359:689–698.

Soberón, J. and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2:1–10.

Stockwell, D. R. B. and D. P. Peters. 1999. The GARP modeling system: problems and solutions to automated spatial prediction. International Journal of Geographical Information Science 13:143–158.

Stockwell, D. R. B. and A. T. Peterson. 2002a. Controlling bias in biodiversity data. Pages 537–546 *in* Predicting species occurrences: issues of scale and accuracy (J. M. Scott, P. J. Heglund, and M. L. Morrison, Editors). Island Press, Washington, D.C., USA.

Stockwell, D. R. B. and A. T. Peterson. 2002b. Effects of sample size on accuracy of species distribution models. Ecological Modelling 148:1–13.

Stockwell, D. R. B. and A. T. Peterson. 2003. Comparison of resolution of methods used in mapping biodiversity patterns from point occurrence data. Ecological Indicators 3:213–221.

Svenning, J.-C. and F. Skov. 2004. Limited filling of the potential range in European tree species. Ecology Letters 7:565–573.

U.S. Department of Interior (USDI). 2001. Hydro-1K elevation derivative data base. USDI, Geological Survey, Washington, D.C., USA. http://edcdaac.usgs.gov/gtopo30/hydro/ (accessed 10 August 2007).

The Wilson Journal of Ornithology 120(4):700–707, 2008

DENSITY AND ABUNDANCE OF MOUNTAIN PLOVERS IN NORTHEASTERN MONTANA

THERESA M. CHILDERS[1,2] AND STEPHEN J. DINSMORE[1,3]

ABSTRACT.—Estimates of local abundance for declining species provide important information necessary for conservation measures. We estimated the density and abundance of Mountain Plover (*Charadrius montanus*) in Phillips and Valley counties in north-central Montana in 2004 using distance sampling methodology. Sampling efforts were stratified to include active prairie dog (*Cynomys* sp.) colonies, an Area of Critical Environmental Concern (ACEC) specifically established for Mountain Plover, and all other habitats. The density of plovers was greatest on prairie dog colonies (7.20 ± 0.42 [SE] plovers/km^2) and much lower on both the ACEC (1.60 ± 0.31 plovers/km^2), and all other habitats (0.07 ± 0.01 plovers/km^2). An estimated 1,028 (95% CI = 903–1,153) plovers inhabited this region in 2004, most (74%) on prairie dog colonies. Our results highlight the importance of prairie dog colonies to plovers in this region and suggest that as much as 10% of their continental population may breed in north-central Montana. *Received 10 September 2007. Accepted 14 February 2008.*

The Mountain Plover (*Charadrius montanus*) is a declining species endemic to the western Great Plains and Colorado Plateau (Knopf 1994, Knopf and Wunder 2006). Historically, its breeding range extended from Canada south along the eastern edge of the Rocky Mountains to New Mexico and east to eastern North Dakota and south to western Texas, including a vast region of short grass prairie, denuded plains, and semi-desert areas (Bent 1929, Knopf and Wunder 2006). Breeding Bird Surveys (BBS) indicate Mountain Plover declined in the 1966–1993 period (Knopf 1996, Knopf and Wunder 2006), although there are no other continent-wide monitoring data for comparison. The Mountain Plover was proposed in 1999 for federal listing as threatened due to concerns over population decline as a result of continued critical habitat loss; listing was denied in 2003 (USDI 2003). However, Mountain Plovers are still considered a species of special concern throughout much of their breeding range (USDA 1994, USDI 2000, Brown et al. 2001) and are one of a suite of the Great Plains ecosystem indicator species that include black-footed ferret (*Mustela nigripes*) and Burrowing Owl (*Athene cunicularia*).

Concerns with continental declines of Mountain Plovers have focused monitoring efforts on estimating their abundance at breeding (Dinsmore et al. 2003, Wunder et al. 2003, Dreitz et al. 2006) and wintering (Knopf and Wunder 2006) sites. The current continental Mountain Plover population estimate is 11,000–14,000 birds (Plumb et al. 2005). Estimates of local abundance are available for key breeding sites and are usually extrapolated from density estimates. Adult density was 2.0 ± 0.46 (SE) plovers/km^2 at the Pawnee National Grasslands, Colorado from 1990 to 1994 (Knopf and Wunder 2006) and an estimated 4,850 adult Mountain Plovers occur in eastern Colorado east of the Front Range (USDI 2003). Plover density on select prairie dog colonies in Phillips County, Montana ranged from 6.80 ± 1.61 (SE) plovers/km^2 in 1991 to 1.28 ± 0.06 (SE) plovers/km^2 in 1995 with an estimated 175 breeding adult Mountain Plovers (Dinsmore 2001, Dinsmore et al. 2003). The density of adult plovers in South Park, Colorado was 7.90 ± 0.90 (SE) plovers/km^2 and an estimated 2,310 breeding adult plovers (Wunder et al. 2003). Plumb et al. (2005) estimated there were 4.47 ± 0.55 (SE) plovers/km^2 in Wyoming and a statewide adult population of 3,393 plovers. Populations in Colorado, Wyoming, and Montana combined comprise the majority of all known breeding Mountain Plovers (Knopf and Miller 1994, USDI 2003).

Estimating and monitoring local abundance of Mountain Plovers throughout their range is important because it identifies concentrations of plovers, helps focus conservation efforts, and aids land management planning by natural

[1] Department of Natural Resource Ecology and Management, 339 Science II, Iowa State University, Ames, IA 50011, USA.

[2] Current address: 24830 West Highway 50, #EC1-E, Gunnison, CO 81230, USA.

[3] Corresponding author; e-mail: cootjr@iastate.edu

resource agencies. Our objectives were to: (1) estimate Mountain Plover density and abundance in 2004 in three habitat strata in southern Phillips and Valley counties, Montana, and (2) suggest how this information can aid management and conservation planning activities to benefit Mountain Plovers.

METHODS

General Study Area.—We studied Mountain Plovers during the 2003 and 2004 breeding seasons in a 7,162-km^2 area in Phillips and Valley counties, Montana (Fig. 1). We used the 2003 breeding season to calculate sampling effort from a pilot study and identify the sampling frame, and then conducted surveys during the 2004 breeding season. Mountain Plovers in Montana primarily select active black-tailed prairie dog (*Cynomys ludovicianus*) colonies for nesting (Knowles et al. 1982, Olson and Edge 1985, Dinsmore 2001). Prairie dog colonies are one of the few remaining suitable habitat types for Mountain Plovers in Montana, and have experienced declines throughout the last century due to large-scale poisoning and sylvatic plague (Olson and Edge 1985, Knowles 1999). Other habitats inhabited by breeding plovers in Montana include areas heavily grazed by domestic sheep in central Montana, and hardpan drainages and a former bentonite mining area in Valley County (Prellwitz 1993, Knowles and Knowles 1998). Plovers are either absent or occur in low densities in Montana outside of these habitats. Our study area consisted primarily of federal lands managed by the Bureau of Land Management (BLM, Glasgow Field Station and Malta Field Office) and the U.S. Fish and Wildlife Service (USFWS, Charles M. Russell National Wildlife Refuge).

We divided the study area into three strata to facilitate surveying plovers. The strata were: (1) a Mountain Plover Area of Critical Environmental Concern (ACEC) in Valley County, (2) all active black-tailed prairie dog colonies in Phillips County (there was none in Valley County), and (3) all other habitats surrounding these strata south of U.S. Highway 2, east of Montana Highway 191, north of the Missouri River, and west of Montana Highway 24 (Fig. 1). Prior research suggested these areas were occupied by plovers at differing densities and stratification was necessary to generate valid estimates of plover abundance.

Mountain Plover ACEC.—The BLM (Glasgow Field Station) established an Area of Critical Environmental Concern in the Little Beaver Creek drainage of Valley County to protect plover breeding habitat and considers the plover a species of special concern (USDI 2000). The ACEC stratum consisted of 10,007 ha delineated by existing roads and property lines, and managed by the BLM to protect Mountain Plover breeding habitat (USDI 2000). The ACEC was comprised of two primary habitats: sparsely vegetated hardpan clay and bentonite soils in drainage bottoms, and densely vegetated gentle rises on either side of the drainages. Mountain Plovers inhabit hardpan soil valley bottoms within the ACEC, where dominant vegetation includes Nuttall's saltbush (*Atriplex nuttallii*), Sandberg bluegrass (*Poa secunda*), western wheatgrass (*Pascopyrum smithii*), plains prickly pear (*Opuntia polycantha*), wild onion (*Allium* spp.), and wild parsley (*Lomatium foeniculaceum*) (USDI 2000). Plovers also use bentonic soils dominated by knotweed (*Polygonum* spp.), Sandberg bluegrass, blue grama (*Bouteloua gracilis*), and western wheatgrass. Gentle rises on either side of valley bottoms are dominated by wild buckwheat (*Polygonum convolvulus*), horizontal juniper (*Juniperus communis*), basin big sagebrush (*Artemisia tridentata tridentata*), and western wheatgrass and are generally not used by Mountain Plovers.

Prairie Dog Colonies.—Breeding Mountain Plovers in north-central Montana are known to selectively inhabit prairie dog colonies and are thought to be restricted to these sites in Phillips County (Knowles et al. 1982, Olson 1984, Dinsmore 2000). Our prairie dog colony stratum consisted of 334 active black-tailed prairie dog colonies ranging from <1 to 308 ha in size comprising a total of 10,515 ha in 2002 (the most recent year colonies were surveyed; J. J. Grensten, pers. comm.). Dominant vegetation in this stratum included fringed sagewort (*Artemisia frigida*), buffalograss (*Buchloe dactyloides*), club moss (*Selaginella densa*), plains prickly pear, blue grama, needle-and-thread grass (*Stipa comata*), and Sandberg bluegrass.

Other Habitats.—All habitat types sur-

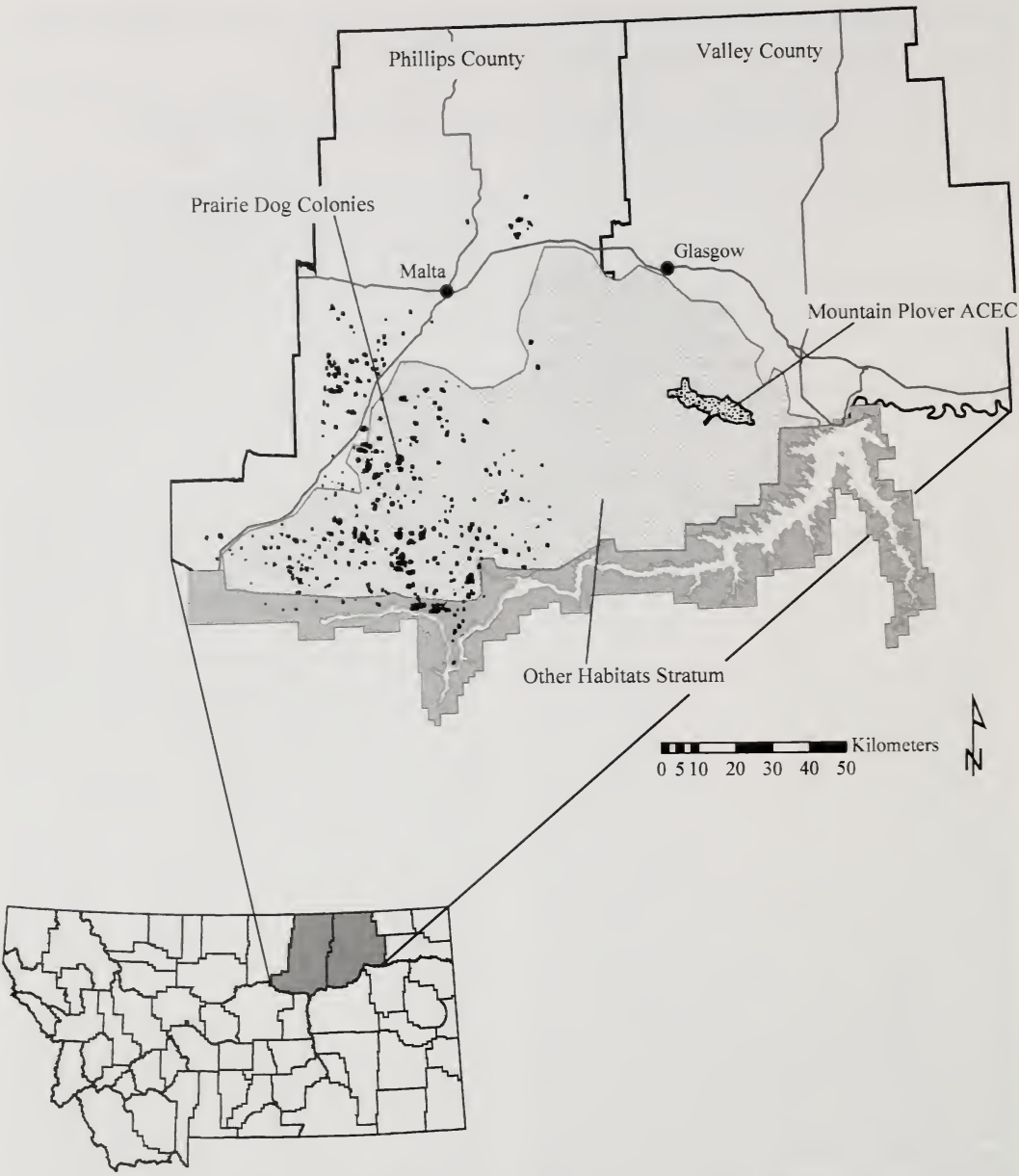


FIG. 1. Phillips and Valley counties, Montana showing strata where breeding Mountain Plovers were surveyed during the 2004 nesting season. The three strata consisted of the Mountain Plover Area of Critical Environmental Concern (ACEC) in Valley County (dark gray stippling), active black-tailed prairie dog colonies in Phillips County (black areas), and all other habitats surrounding the prairie dog colony and ACEC strata (light gray stippling).

rounding the prairie dog colony and ACEC strata in southern Phillips and Valley counties were included in the 'other habitats stratum' (716,241 ha). We sampled all habitats in this stratum and made no attempt to partition the sample based on suitable habitat because: (1) we did not have access to GIS information with sufficient detail to identify suitable plover habitat, and (2) logistical constraints prevented us from mapping suitable habitat in the

field during this study. Our purpose for sampling this region was to provide baseline information about Mountain Plover density outside the other two strata. The other habitats strata varied in topography from the rolling Larb Hills to relatively flat open rangeland. Vegetation was generally taller and denser compared to that of the other two strata, but comprised of the same species. Small areas of habitat similar to those in the ACEC were scattered throughout both counties.

Statistical Analyses.—We used radial distance point count surveys (Buckland et al. 2001) to sample Mountain Plovers in each of the three strata. We used data from pilot studies to calculate a suitable sample of points given a 15% desired coefficient of variation (CV). Distance sampling encounter rates from the 1991–2000 breeding seasons (SJD, unpubl. data) for the prairie dog colony stratum were used to calculate a suitable survey sample (n = 105 points). We conducted randomly located point count surveys in early May 2004 in the ACEC stratum and used the resulting encounter rates to delimit the survey sample for the ACEC (n = 110 points).

The number of sample points in the other habitats strata was chosen to be logistically feasible and to provide baseline evidence regarding plover density. We knew this stratum supported a low density of Mountain Plovers, based on personal observation and consultation with regional biologists, and concluded that an excessive number of sample points was needed to generate a precise abundance estimate. Generating a plover abundance estimate with reliable precision was not possible in this stratum given time, personnel, and logistical constraints. However, we believed it was necessary to provide some evidence regarding Mountain Plover density in the other habitats stratum. A generally recommended sample size for areas with relatively good probability of detection of animals is 40 (Buckland et al. 2001). We believed probability of detecting plovers was low to moderate in this stratum due to shrub cover and rolling topography. We chose to survey slightly more (n = 50 points) than the recommended number of sample points to provide evidence, rather than a precise estimate, of Mountain Plover density for this stratum.

We overlaid a 500 × 500 m grid with a random starting point on the ACEC and other habitats strata, and randomly selected grid center point coordinates for survey points. We chose survey points differently for the prairie dog stratum because of how colonies were distributed on the landscape. The borders of all colonies were mapped in 2002 with GPS units by the BLM (Malta Field Office). We selected colonies at random with replacement, assigned survey points proportional to colony size, and spaced points equidistant within a colony if it included >1 point.

One observer (TMC) visited all points in the ACEC (mid-May through mid-Jun) and other habitats strata (mid-Jun through early Jul) while a second observer (SJD) visited all points on prairie dog colonies (mid-May through early Jun) to minimize observer bias. Timing of all surveys coincided with the nesting season in Montana (Dinsmore et al. 2002) but we visited the ACEC and other habitats strata at slightly different seasons for logistical reasons. Individual points were located on the ground using a Garmin Explorer V GPS unit and were approached by vehicle. Plovers actively avoid a person on foot but appear to ignore vehicles (pers. obs.). We minimized violation of the assumption that there was no avoidance behavior by approaching survey points in a vehicle. All surveys were conducted during daylight hours (0500 to 1200 hrs MDT) during standardized weather conditions (0–24 km/hr wind speed, no precipitation, and temperature <27° C). Surveys were conducted in the early portion of the breeding season to ensure that only breeding adults were included, and there were no problems with post-breeding dispersal. We visited each point for 5 min, surveyed for plovers using 10 × 40 binoculars, and measured the distance (m) to each Mountain Plover using a NewCon Optic LRM 1500 laser rangefinder. All measurements were exact and we used actual distances rather than placing observations into distance groups. Observations were treated as statistically independent events, which is reasonable given that 43% of sightings were of a single bird.

We used Program DISTANCE (Version 3.5; Thomas et al. 1998) to model detection rates of plovers and calculate stratum-specific density estimates. We considered the four robust models best suited for detection functions sug-

TABLE 1. Model selection results from Program DISTANCE, and density ($\hat{D}$; birds/km^2) and abundance ($\hat{N}$) estimates for Mountain Plovers on the Area of Critical Environmental Concern (ACEC) and active black-tailed prairie dog colonies in north-central Montana, 2004.

Model, expansion	AIC	ΔAIC	$\hat{D}$	$\hat{N}$	CV
ACEC					
Uniform, cosine[a]	658.76	0.00	1.60	160	24%
Half-normal, hermite	666.74	7.98			
Uniform, simple polynomial	751.16	92.40			
Hazard rate, cosine	777.27	118.51			
Prairie dog colonies					
Hazard rate, cosine[b]	3792.75	0.00	7.20	758	6%
Half-normal, hermite	3796.22	3.47			
Uniform, simple polynomial	3870.75	78.00			
Uniform, cosine	17,453.01	13,660.26			

[a] Four cosine expansion terms.
[b] Zero cosine expansion terms.

gested by Buckland et al. (2001:155): (1) uniform key function with a cosine expansion, (2) uniform key function with a simple polynomial expansion, (3) half-normal key function with a hermite expansion, and (4) hazard rate key function with a cosine expansion. All models exhibit properties that meet the distance sampling assumption that probability of detection of an animal declines with increasing distance from the point. Model fit was assessed using the Chi-square goodness-of-fit test in Program DISTANCE. We used AIC model selection (Burnham and Anderson 2002) to select the best approximating model for each stratum.

There were insufficient plover detections (1 detection in 50 point surveys) in the other habitats stratum, and density and abundance estimates were calculated using the ACEC detection function. We chose this approach for three reasons: (1) we wanted to generate an estimate of abundance for this stratum for planning purposes and were unable to entirely ignore the small sample size; (2) both the ACEC and other habitats strata surveys were conducted with the same observer, and pooling these data into a single detection function seemed reasonable; and (3) portions of these two regions had similar habitat types, making them more similar than the other habitats stratum was to the prairie dog colony stratum.

Abundance.—Plover density estimates in the prairie dog colony and ACEC strata were multiplied by their known areas to calculate stratum-specific estimates of Mountain Plover abundance. We estimated plover abundance differently for the other habitats stratum. Rather than estimate abundance for all habitats in this stratum, we chose to focus only on suitable habitat. We used previously classified (shrub, non-shrub, bare ground, and water) Landsat 7 (14 May 2003, path 37, rows 26 and 27) satellite imagery to identify potential Mountain Plover habitat. We considered potential Mountain Plover habitat at this scale to consist of either non-shrub or bare ground patches. Olson-Edge and Edge (1987) observed that Mountain Plovers in Montana select prairie dog colonies >6 ha in size. Thus, we restricted potential habitat by selecting patches >6 ha (area = 157,573 ha). The vegetation structure of non-shrub patches could not be calculated from satellite images, and not all of the area identified actually contained suitable plover nesting habitat. We estimated that 22% (157,573 ha) of this stratum contained suitable Mountain Plover habitat based on these criteria.

RESULTS

Model Selection and Detection Function.—The best model selected for the ACEC was a uniform key function with a cosine expansion and for the prairie dog colony stratum it was the hazard rate key function with a cosine expansion (Table 1); no other models were considered competing ($\Delta AIC < 2$). Both of these models fit the data well ($P > 0.15$). We were unable to develop a detection function for the

other habitats stratum due to the low detection rate (1 detection in 50 points).

Density and Abundance Estimates.—The density of Mountain Plovers was greater in the prairie dog colony stratum ($\hat{D}$ = 7.20 plovers/km^2, 95% CI = 0.064–0.082, 6.41% CV) than in the ACEC stratum ($\hat{D}$ = 1.60 plovers/km^2, 95% CI = 0.010–0.025, 24.03% CV). The majority (74%) of the Mountain Plovers within the study area occurred in the prairie dog colony stratum ($\hat{N}$ = 758, 95% CI = 668–860) with smaller numbers in the ACEC ($\hat{N}$ = 160, 95% CI = 100–285). The density of Mountain Plovers in the other habitats stratum was two orders of magnitude less than the density in the other two strata ($\hat{D}$ = 0.07 plovers/km^2, 95% CI = 0.0005–0.0010, 16.54% CV). An optimistic estimate of Mountain Plover abundance in this stratum was relatively low for such a large area ($\hat{N}$ = 110, 95% CI = 78–154).

DISCUSSION

We estimated Mountain Plover density in three habitats in north-central Montana. The density estimate for the prairie dog colony stratum had good precision (6.41% CV) due to robustness of the data used to generate the detection function. The precision of the ACEC density estimate was less than expected (24% CV vs. a desired 15% CV) and may have resulted because suitable habitat occurred in small and unevenly distributed patches. The density of Mountain Plovers in the other habitats stratum was thought to be low prior to this survey, and an infeasible number of point counts would have been necessary to produce an estimate with good precision. Our result for this stratum should be interpreted with caution.

Sampling issues caused us to make key assumptions about plover detection rates and suitable plover habitat in the other habitats strata. The ACEC and other habitats strata shared some habitat characteristics, e.g., densely vegetated low ridges interspersed with irregular patches of suitable Mountain Plover habitat. Thus, the calculated density for the other habitats stratum appeared to realistically represent Mountain Plover density in regions similar to the ACEC. The scale and frequency of suitable habitat patches varied between strata, and we corrected for an inflated abundance estimate in the other habitats stratum by constricting the inferential space to only the area of potential plover habitat. It is unlikely that all identified potential plover habitat (22%, or 157,573 ha) is actually suitable for nesting.

There are few rigorous estimates of Mountain Plover abundance in Montana. A specific sampling protocol has been used on a portion of prairie dog colonies in southern Phillips County (Dinsmore 2001), but our study presents the first formal sample of Mountain Plover density and abundance throughout a significant proportion of its northeastern Montana breeding range. Mountain Plover density in the prairie dog stratum was much greater than densities reported for grasslands in Colorado (2.0 ± 0.46 birds/km^2 to 4.7 ± 1.20 birds/km^2; Knopf and Wunder 2006), and for grasslands (5.17 ± 1.06 birds/km^2) and shrub-steppe habitats (4.23 ± 0.67 birds/km^2) in Wyoming (Plumb et al. 2005). Our density estimates were similar to those reported from Phillips County in the early 1990s (SJD, pers. obs.), despite an outbreak of sylvatic plague in the mid-1990s that decimated prairie dogs (and affected plover habitat) throughout this region (Dinsmore et al. 2005). The majority of Mountain Plovers currently breeding in southern Phillips and Valley counties (74%) inhabit active black-tailed prairie dog colonies. The strong link between plovers and prairie dogs in Montana (Dinsmore et al. 2005), which is not as prevalent elsewhere in the plover's range suggests that size and mosaic of suitable plover habitat patches may be more dynamic in short-grass prairie habitats at other sites. Other forms of disturbance such as fire and grazing by ungulates creates suitable plover nesting habitat in areas where prairie dogs do not constantly maintain low vegetation.

Our investigation of Mountain Plover abundance outside prairie dog colonies and ACEC strata partially confirms biologists' contention that the other habitats stratum is mostly uninhabited by plovers. An optimistic estimate of plover abundance in all potential nesting habitat within the other habitats stratum is 110 plovers, which may comprise up to 10% of the breeding population in southern Phillips and Valley counties.

Our study revealed that plovers breeding

near the northern limit of their range in Montana constitute a significant proportion of this species' overall population and should remain a conservation priority. The total population estimate of Mountain Plovers in southern Phillips and Valley counties was 1,028 adults (95% CI = 903–1,153, 6.18% CV), or less than 10% of the estimated 11–14,000 Mountain Plovers in North America (USDI 2003, Plumb et al. 2005). Most inhabit active prairie dog colonies in Phillips County. With removal of large-scale grazers and increased fire control, sites maintained by prairie dog activities and unproductive soils have become the only suitable areas available to breeding Mountain Plovers in much of Montana.

CONSERVATION IMPLICATIONS

Our study provides critical baseline information about plover density and occurrence in Phillips and Valley counties in north-central Montana, but more investigation of plovers in this region is needed. Patches of breeding habitat outside of the prairie dog colony and ACEC strata should be identified and sampled more intensively to gain a more precise estimate of plover abundance. Our investigation of the other habitats stratum suggests it may support up to 10% of the Mountain Plover population in Phillips and Valley counties. Much of the suitable plover habitat in this stratum appears to be near the ACEC, suggesting that Mountain Plovers may benefit from an expansion of the ACEC. Mountain Plover abundance within the prairie dog colony and ACEC strata should be monitored at regular intervals. Plovers in both of these regions represent important contributions to the continental population, are considered indicators of the health of their respective habitats (Dinsmore 2000), and should continue to be the focus of local monitoring efforts and management.

Regional population estimates of breeding Mountain Plovers contribute useful information for conservation planning at both the regional and continental levels. Recently, researchers have estimated abundance of Mountain Plovers in South Park, Colorado (Wunder et al. 2003), eastern Colorado (Tipton 2007), and in Wyoming (Plumb et al. 2005). These estimates, combined with information from other breeding populations, suggest the continental population of Mountain Plovers is greater than previously believed (Plumb et al. 2005, Knopf and Wunder 2006). The previous continental population estimate based on samples of wintering plovers was 5,000–10,000 individuals; Plumb et al. (2005) suggests a revised population estimate of 11,000–14,000 individuals.

The ACEC and active prairie dog colonies provide nesting habitat for the majority of Mountain Plovers in north-central Montana. Local managers should continue to (1) protect the ACEC and active prairie dog colonies on public lands from major human disturbances, such as mining, during the plover breeding season, and (2) monitor the size and health of suitable plover habitat in each region (hardpan flats in Valley County and active prairie dog colonies in Phillips County).

ACKNOWLEDGMENTS

We thank the U.S Bureau of Land Management (Glasgow Field Office) for funding this study. David Waller, John Carlson, John Fahlgren, and many other staff from the Glasgow Field Office provided field assistance. J. J. Grensten and C. T. Wilcox helped with fieldwork in Phillips County and M. D. Smith provided assistance with GIS work.

LITERATURE CITED

Bent, A. C. 1929. Life histories of North American shorebirds. U.S. National Museum Bulletin 146: 263–269.

Brown, S., C. Hickey, B. Harrington, and R. Gill (Editors). 2001. The U.S. Shorebird Conservation Plan. Second Edition. Manomet Center for Conservation Sciences, Manomet, Massachusetts, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York, USA.

Dinsmore, S. J. 2000. Mountain Plover. Pages 213–218 *in* Endangered animals: a reference guide to conflicting issues (R. P. Reading and B. Miller, Editors). Greenwood Press, Westport, Connecticut, USA.

Dinsmore, S. J. 2001. Population biology of Mountain Plovers in southern Phillips County, Montana. Dissertation. Colorado State University, Fort Collins, USA.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002.

Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2003. Annual survival and population estimates of Mountain Plovers in southern Phillips County, Montana. Ecological Applications 13:1013–1026.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2005. Mountain Plover population responses to black-tailed prairie dogs in Montana. Journal of Wildlife Management 69:1546–1553.

Dreitz, V. J., P. M. Lukacs, and F. L. Knopf. 2006. Monitoring low density avian populations: an example using Mountain Plovers. Condor 108:700–706.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247–257.

Knopf, F. L. 1996. Prairie legacies—birds. Pages 135–148 *in* Prairie conservation: preserving North America's most endangered ecosystem (F. B. Samson and F. L. Knopf, Editors). Island Press, Covelo, California, USA.

Knopf, F. L. and B. J. Miller. 1994. *Charadrius montanus*—montane, grassland, or bare-ground plover? Auk 111:504–506.

Knopf, F. L. and M. B. Wunder. 2006. Mountain Plover (*Charadrius montanus*). The birds of North America. Number 211.

Knowles, C. J. 1999. Selective use of black-tailed prairie dog colonies by Mountain Plovers—a second look. USDI, Bureau of Land Management, Malta Field Office, Malta, Montana, USA.

Knowles, C. J. and P. R. Knowles. 1998. The historic and current status of the Mountain Plover in Montana. USDI, Bureau of Land Management, Malta Field Office, Malta, Montana, USA.

Knowles, C. J., S. P. Stoner, and S. P. Gieb. 1982. Selective use of black-tailed prairie dog towns by Mountain Plovers. Condor 84:71–74.

Olson, S. L. 1984. Density and distribution, nest site selection, and activity of the Mountain Plover on the Charles M. Russell National Wildlife Refuge. Thesis. Montana State University, Bozeman, USA.

Olson, S. L. and D. Edge. 1985. Nest site selection by Mountain Plovers in north central Montana. Journal of Range Management 38:280–282.

Olson-Edge, S. L. and W. D. Edge. 1987. Density and distribution of the Mountain Plover on the Charles M. Russell National Wildlife Refuge. Prairie Naturalist 19:233–238.

Plumb, R. E., F. L. Knopf, and S. H. Anderson. 2005. Minimum population size of Mountain Plovers breeding in Wyoming. Wilson Bulletin 117:15–22.

Prellwitz, D. M. 1993. Additional Mountain Plover sightings in Montana. Prairie Naturalist 25:23–26.

Thomas, L., J. L. Laake, J. F. Derry, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. Strindberg, S. L. Hedley, M. L. Burt, F. F. C. Marques, J. H. Pollard, and R. M. Fewster. 1998. Distance 3.5. Release 6. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, United Kingdom.

Tipton, H. C. 2007. Occupancy, abundance, and density of Colorado breeding grassland birds: estimation and habitat correlations. Thesis. Colorado State University, Fort Collins, USA.

U.S. Department of Agriculture (USDA). 1994. Final environmental impact statement for management strategy for Mountain Plover. USDA, Forest Service, Pawnee National Grasslands, Greeley, Colorado, USA.

U.S. Department of Interior (USDI). 2000. Bitter Creek and Mountain Plover areas of critical environmental concern plan amendment and environmental assessment. MT-096-99-04. USDI, Bureau of Land Management, Glasgow Field Station, Glasgow, Montana, USA.

U.S. Department of the Interior (USDI). 2003. Endangered and threatened wildlife and plants: withdrawal of the proposed rule to list the Mountain Plover as threatened. Federal Register 68:53083–53101.

Wunder, M. B., F. L. Knopf, and C. A. Pague. 2003. The high-elevation population of Mountain Plovers in Colorado. Condor 105:654–662.

The Wilson Journal of Ornithology 120(4):708–716, 2008

LAND COVER ASSOCIATIONS OF NESTING TERRITORIES OF THREE SYMPATRIC *BUTEOS* IN SHORTGRASS PRAIRIE

SCOTT McCONNELL,[1,4,5] TIMOTHY J. O'CONNELL,[2] AND DAVID M. LESLIE JR.[3]

ABSTRACT.—Three species of *Buteo* hawks nest sympatrically in the southern Great Plains of the United States. Dietary overlap among them is broad and we tested the hypothesis these species partition their breeding habitat spatially. We compared land cover and topography around 224 nests of the three species breeding in shortgrass prairie in 2004 and 2005. Red-tailed Hawks (*Buteo jamaicensis*) nested almost exclusively in riparian timber surrounded by prairie (95% prairie land cover around nests) and disproportionately used areas with greater topographic relief within prairie landscapes. Swainson's Hawks (*B. swainsoni*) commonly nested in low-relief areas dominated by small-grain production agriculture but generally used habitats in proportion to availability. Most nest sites of Ferruginous Hawks (*B. regalis*) were in prairie (78% prairie land cover around nests), but some were in areas that were at least partially agricultural. Ferruginous Hawks had at least two times more sand sagebrush (*Artemisia filifolia*) around their nests than their two congeners. We conclude that sympatric breeding *Buteos* on the southern Great Plains spatially partitioned nest sites according to subtle differences in land cover and topography. *Received 12 March 2007. Accepted 17 February 2008.*

Species with similar ecological niches may compete for vital resources. Pianka (1974) warned against the assumption that niche overlap indicates competition because abundant resources and/or niche modification could make competition irrelevant. Jaksic and Braker (1983) concluded that diurnal raptors do not adjust their diets because of competition, but rather partition their habitat use via agonistic encounters. This was supported by observations of sympatric Swainson's (*Buteo swainsoni*) and Harris's (*Parabuteo unicinctus*) hawks in New Mexico where overlap of prey species remained high even as prey biomass declined, and Swainson's Hawks aggressively excluded Harris's Hawks from their territories (Gerstell and Bednarz 1999).

In western North America, Red-tailed (*Buteo jamaicensis*), Swainson's, and Ferruginous (*B. regalis*) hawks breed sympatrically in shortgrass prairies in the southern Great Plains. These species are diurnal predators that seek elevated nest sites (Preston and Beane 1993, Bechard and Schmutz 1995, England et al. 1997); thus, they may compete for breeding territories. From studies in Oregon (Cottrell 1981), Washington (Bechard et al. 1990), and Alberta (Schmutz et al. 1980), authors concluded that sympatrically breeding Red-tailed, Ferruginous, and Swainson's hawks coexisted by partitioning space, not prey. Habitat relationships in the southern Great Plains have received comparatively less attention, but Giovanni et al. (2007) found high dietary overlap between Swainson's and Ferruginous hawks in southern Cimarron County, Oklahoma, and two adjacent counties in Texas (Dallam) and New Mexico (Union).

The Red-tailed Hawk is a widely distributed breeder in Oklahoma (Reinking 2004). Ferruginous and Swainson's hawks are more restricted in their breeding range in Oklahoma with Swainson's Hawks largely confined to the western half of the state and Ferruginous Hawks mostly in Texas and Cimarron counties in the Panhandle (Reinking 2004). Understanding distributions and dynamics of these species is a goal of the Oklahoma Comprehensive Wildlife Conservation Strategy (ODWC 2005) in which Swainson's and Ferruginous hawks are listed as Tier I and II conservation priorities, respectively. Swainson's Hawk has been listed as a species of conser-

[1] Department of Zoology, 430 Life Sciences West, Oklahoma State University, Stillwater, OK 74078, USA.

[2] Department of Natural Resource Ecology and Management, 240 Agriculture Hall, Oklahoma State University, Stillwater, OK 74078, USA.

[3] Oklahoma Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, 404 Life Sciences West, Oklahoma State University, Stillwater, OK 74078, USA.

[4] Current address: 330A Pahlow Lane, Laramie, WY 82070, USA.

[5] Corresponding author; e-mail: scott.mcconnell1@yahoo.com

vation concern at the continental scale (Rich et al. 2004).

We examined the spatial partitioning of breeding territories among all three *Buteos* in shortgrass prairie due to the potential niche overlap and the propensity for Swainson's Hawks to aggressively exclude other species (Schmutz et al. 1980, Janes 1994). Our objectives were to quantify and compare land cover, topography, and other features around nests to test the hypothesis the three sympatric *Buteo* species partition space in the southern Great Plains.

METHODS

Study Area.—We conducted this study in Cimarron County, Oklahoma within the Shortgrass Prairie Bird Conservation Region (Rich et al. 2004) and the Western Short Grasslands Ecoregion (Ricketts et al. 1999). Cimarron County occupies 4,769 km^2 at 1,090–1,518 m elevation, increasing from east to west. Most of the area is flat, but the northwestern part of the county is dominated by mesas, including Black Mesa, the highest point in Oklahoma. Average annual precipitation in the Boise City area was 47 cm from 1971 to 2000 (NOAA 2002).

Ninety-six percent of Cimarron County was farmland in 2002 of which cropland occupied 40% and rangeland 56% of the land area. Crops and area harvested in 2002 were: sorghum, 236 km^2; winter wheat, 228 km^2; corn, 88 km^2; and forage (hay, etc.), 65 km^2 (USDA 2004). Many of the agricultural areas had center-pivot irrigation systems drawing on the Ogalalla Aquifer. Cimarron County had 641 km^2 enrolled in the Conservation Reserve Program (CRP) in 2004 (P. G. Toon, USDA, pers. comm.).

Historically, the Western Short Grasslands were characterized by buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) prairie; pastures dominated by these grasses persist in Cimarron County (Ricketts et al. 1999). Sand sagebrush (hereafter sandsage) (*Artemisia filifolia*) and plains yucca (*Yucca glauca*) are common on well-drained soils (Tyrl et al. 2002).

Trees are limited to riparian zones and around human settlements. The Cimarron River flows through the northern half of the county and the Beaver River bisects the southern half (Fig. 1). Plains cottonwoods (*Populus deltoides*) and dense stands of salt cedar (*Tamarix gallica*) occur in riparian areas; Siberian elms (*Ulmus pumilla*) have been planted as windbreaks around homesteads.

Nest Searches.—We conducted opportunistic nest searches from early May to early July in 2004 and 2005, and located nests while driving county roads and walking ranches and river courses. We found some nests in the course of doing unrelated field work. Our total search effort included coverage of ≥50% of the sections (259 ha/section) in Cimarron County.

We considered only active nests in our analysis, defining "active" as the presence of juveniles or ≥1 incubating adult. A nest site used by the same species 2 years in succession was considered independent between years. Over 80% of the locations were plotted using a GPS unit (Garmin Geko 201, Garmin International, Olathe, KS, USA); we plotted the remainder in a GIS by finding the location of the nest tree on an aerial photograph after recording the legal location (township, range, 1/4-section) in the field. We recorded nest tree species at most locations.

GIS Analysis.—We imported all Cimarron County nest locations into ArcMap 9 (ESRI, Redlands, CA, USA), and created buffers of 500-, 1,000-, and 2,000-m radii (79-, 314-, and 1,256 ha) around nest locations. We placed the same buffers around 54 random points generated in the GIS with a Hawth's Tools function (Beyer 2004). We used these three spatial extents to permit comparisons ranging from the immediate vicinity of the nest (79 ha) to an extent (314–1,256 ha) roughly the size of the home ranges reported for the three hawk species (Bechard 1982, Andersen and Rongstad 1989, Woodbridge 1991, Bechard and Schmutz 1995, Leary et al. 1998).

We imported the 1992 National Land Cover Dataset (NLCD) for Cimarron County from the USGS Seamless Data Distribution System (SDDS) web site (USGS 2004) into ArcMap and merged it with a layer delineating 2005 CRP land that was provided by the Cimarron County Farm Service Agency (NRCS) (Fig. 1). We combined potentially redundant features from the NLCD into a smaller number of more general categories. We renamed the

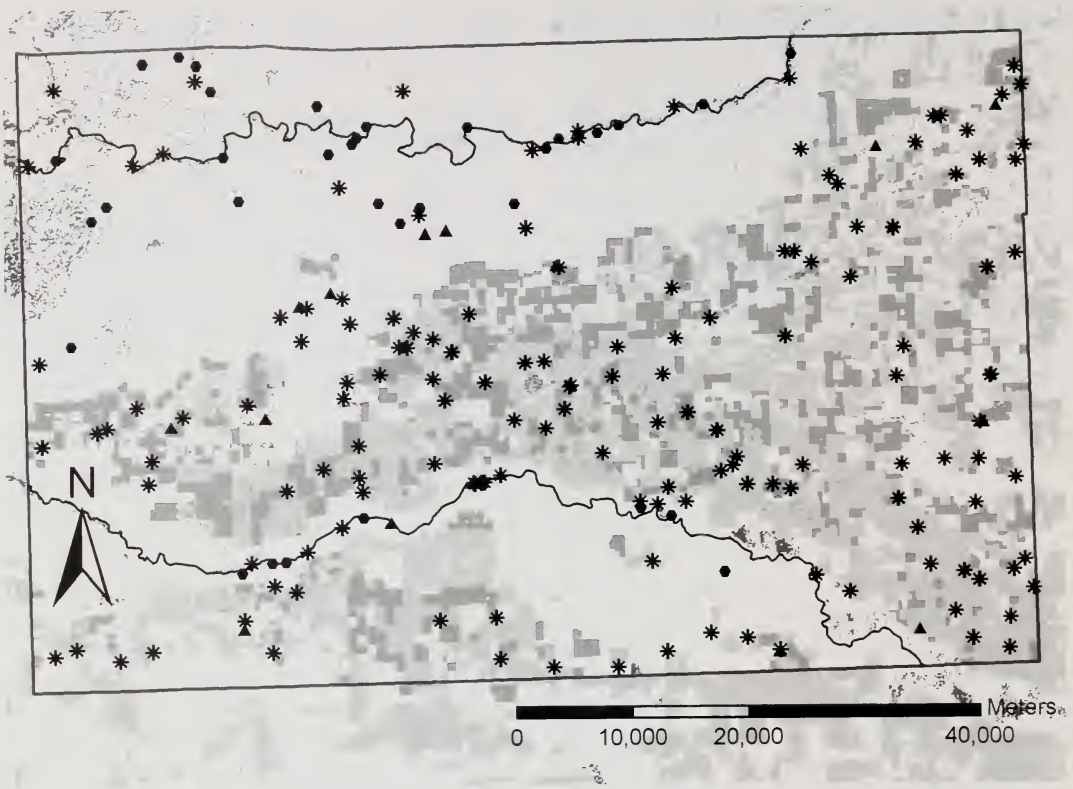


FIG. 1. Land cover map of Cimarron County, Oklahoma, compiled from National Land Cover Dataset and Conservation Reserve Program data layers illustrating nest locations in 2004–2005 for Swainson's (stars), Ferruginous (triangles), and Red-tailed hawks (hexagons). White areas represent prairie; gray indicates agricultural areas, with CRP areas darker; lightly stippled areas (e.g., northwestern corner) represent wooded vegetation.

grasslands/herbaceous designation "prairie" and combined pasture/hay, row crops, and small grains into "agriculture," and all forested and shrubland categories into "wooded." The latter grouping was necessary because many riparian areas in Cimarron County were heavily lined with large cottonwoods, some of which were classified as "shrubland" by the NLCD.

We used Oklahoma Gap Analysis Project (GAP; Fisher and Gregory 2001) data in a separate analysis to analyze sandsage land cover around nests. There are large areas of sandsage in Cimarron County which, if recognized by the NLCD, are generally classified as "shrubland;" there is no distinct category for sandsage prairie in the NLCD.

We performed land cover analyses by clipping the nest-area and random point buffers to the NLCD/CRP and GAP layers and using a raster summary function tool in the GIS to derive the total number of the different land cover type pixels in each buffer. Raster summary results for each buffer were summed to derive the total land cover proportion for each species/random point at each extent. We also compared the NLCD/CRP classifications of 100 GIS-generated random points with a National Agriculture Imagery Program (NAIP) 2003 photograph (USDA 2003) to test the accuracy of the NLCD/CRP land cover categories.

We used the same buffers (79-, 314-, and 1,256 ha) created for land cover analysis to investigate topography around each nest site and random point. We imported a Digital Elevation Model (DEM) from the USGS SDDS web site (USGS 2004) and analyzed the "mean maximum slope" for all buffers. In this operation, using Hawth's Tools (Beyer 2004) and ArcMap's Spatial Analyst, the GIS calculated a slope percentage for each 30 ×

30 m pixel in each nest site (or random point) buffer. The largest value in the buffer was designated the maximum slope percentage for that buffer. We calculated the mean of the maximum slope across all pixels in each buffer for all nests of each species (and for all random points). The resulting mean of the maximum slope provided an indication of features such as cliffs and rock outcrops, and we compared the maximum slope percentage means for all species and random points. We also used the DEM to compare elevation at each nest site and random point.

Statistical Analyses.—We analyzed mean percent cover for prairie, CRP, wooded, and, using GAP data, sandsage around *Buteo* nests and 54 random points. We did not include agricultural land cover in our analysis because prairie and agricultural layers were strongly negatively correlated ($r = -0.83$) in a preliminary analysis of total Cimarron County landcover. We tested for land cover and topography differences with one-way analyses of variance (ANOVA). We compared median values using Mann-Whitney or Kruskal-Wallis tests when Levene's tests for equal variances indicated unequal variances that could not be stabilized with data transformations. All tests were performed at $\alpha = 0.05$ in Minitab 13.20 (Minitab Inc. 2000).

RESULTS

We found 168 Swainson's, 38 Red-tailed, and 18 Ferruginous hawk nests during 2004 and 2005 (Fig. 1). Fourteen of 18 Ferruginous (78%), 33 of 38 Red-tailed (87%), and 148 of 168 (88%) Swainson's hawk nest locations analyzed represented locations recorded in only one of the two field seasons, because we made efforts to find new nest locations during the second field season.

Land cover percentages surrounding nests and random points did not differ at the 79-, 314-, and 1,256-ha scales, except the wooded component around Red-tailed Hawk nests ($F_{2,95} = 3.5$, $P = 0.035$). Percent cover of wooded habitat around Red-tailed Hawk nests, however, only ranged from 2 to 4% across the three scales. We selected the 314-ha scale for comparisons among nests of the different species and random points due to the overall similarities in landcover composition at the three scales. The land cover layer was 98% accurate in the test of 100 random points; there were two misclassifications and 12 instances where accuracy could not be measured by comparison with the NAIP photograph.

Variances for Red-tailed Hawk nests were smaller than for the other two *Buteos* and random points because of similar land cover composition around all Red-tailed Hawk nests. Levene's tests on transformed means indicated unequal variances when mean cover of CRP, prairie, and wooded vegetation for Red-tailed Hawk nests were included in the analysis; variances were equal when means for these three land cover types were excluded. Thus, we tested for differences in mean CRP, prairie, and wooded vegetation between Swainson's and Ferruginous hawk nests and random points with ANOVA and used nonparametric tests to examine differences with Red-tailed Hawk nests. Untransformed means for sandsage cover had equal variances with all three species and the random points included.

We found no differences in percent CRP among random points and nest locations for Swainson's and Ferruginous hawks ($F_{2,240} = 1.0$, $P = 0.37$). A Kruskal-Wallis test including Red-tailed Hawk nests indicated a difference ($H_3 = 41.0$; $P < 0.001$; df = 3) with less CRP surrounding Red-tailed Hawk nests (Fig. 2).

Prairie cover differed among random points and locations for Swainson's and Ferruginous hawk nests ($F_{2,240} = 5.9$, $P = 0.003$); a Tukey's confidence interval comparison indicated that, while nest buffers for neither species differed significantly from random sites, prairie cover around nests of the two species differed from each other. A Mann-Whitney test for the difference in prairie cover between Red-tailed and Ferruginous hawks was not significant ($U = 445$, $P = 0.24$), but the difference was significant comparing Red-tailed and Swainson's hawk nests ($U = 15116$, $P < 0.001$), and to random points ($U = 2045$, $P < 0.001$) (Fig. 2).

The proportion of wooded cover was similar among random points and nest locations for Swainson's and Ferruginous hawks ($F_{2,240} = 0.6$, $P = 0.57$). A Kruskal-Wallis test including Red-tailed Hawk nests indicated a difference ($H_3 = 49.8$, $P < 0.001$). Wooded cover was highest around nests for Red-tailed

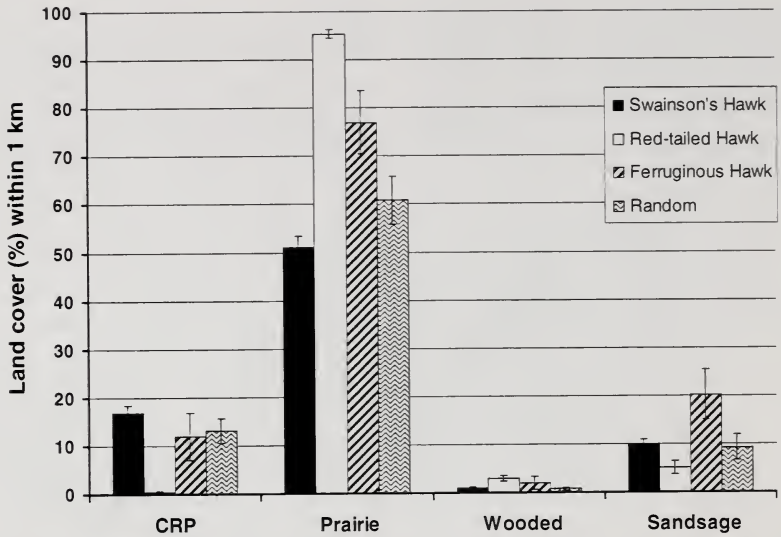


FIG. 2. Mean ± SE land cover percentages within 1 km (314 ha) of Swainson's (n = 168), Red-tailed (n = 38), and Ferruginous (n = 18) hawk nests, and 54 random points in Cimarron County, Oklahoma. Sandsage percentages were calculated from a different GIS layer and totals can exceed 100%.

Hawks because this species nested in relatively continuous riparian forest rather than in isolated trees as did the other two *Buteos* (Fig. 2).

Sandsage cover was higher around Ferruginous Hawk nests compared with the other *Buteo* species ($F_{3,278}$ = 3.6; P = 0.013; Fig. 2), but did not differ from sandsage cover around random points (Tukey's confidence interval included zero). We found no differences between any of the other species or random points.

Mean maximum slope differed within species at the different buffer scales (Table 1; $F \geq 3.4$; df $\geq$ 53; $P \leq 0.035$; all tests summarized) and we compared the log-transformed means among species across all three scales independently. The mean maximum slope around Red-tailed Hawk nests was higher than for its congeners and random points at all scales; Swainson's and Ferruginous hawks did not differ from random points (Table 2). Mean nest elevation ranged from 1,239 to 1,256 m and did not differ among species ($F_{3,279}$ = 0.4; P = 0.76).

We examined topographic relief around nests of Red-tailed Hawks to learn if the higher maximum slope was an artifact of this species nesting disproportionately in prairie (higher relief) than in cultivated areas (lower relief), or if Red-tailed Hawks were associated with areas of especially high relief within prairie. We compared mean maximum slope around Red-tailed Hawk nests at the 314-ha scale with a "prairie"-classified subset (n = 57) of the 100 random points used to verify NLCD/CRP accuracy. Means for Red-tailed Hawk nests were higher ($F_{1,94}$ = 13.2; $P <$ 0.001).

Eight Swainson's Hawk nests were ≤2 km

TABLE 1. Mean ± SE maximum slope percentages in 79-, 314-, and 1,256-ha buffers around Swainson's (n = 168), Red-tailed (n = 38), and Ferruginous (n = 18) hawk nests and random points (n = 54) in Cimarron County, Oklahoma.

Sites	79 ha	314 ha	1,256 ha
Swainson's Hawk	6.21 ± 0.58	8.96 ± 0.84	12.32 ± 1.09
Red-tailed Hawk	27.52 ± 3.11	35.80 ± 3.31	45.83 ± 3.85
Ferruginous Hawk	9.84 ± 1.49	11.94 ± 1.51	16.76 ± 2.14
Random	9.92 ± 1.78	13.39 ± 2.10	17.90 ± 2.54

TABLE 2. Between species comparisons for mean maximum slope in 79-, 314-, and 1,256-ha buffers around Swainson's (n = 168), Red-tailed (n = 38), and Ferruginous (n = 18) hawk nests and random points (n = 54) in Cimarron County, Oklahoma. ANOVA comparisons between species and random points, and Tukey intervals, are given for each scale; * indicates $P < 0.05$.

Comparison	79 ha	314 ha	1,256 ha
	$F_{3,278} = 35.9$ $P < 0.001$	$F_{3,278} = 37.7$ $P < 0.001$	$F_{3,278} = 38.4$ $P < 0.001$
Swainson's vs. Red-tailed	−0.8904 −0.5350*	−0.8652 −0.5275*	−0.8134 −0.4977*
Swainson's vs. Ferruginous	−0.49667 −0.0059*	−0.4472 0.0191	−0.4465 −0.0104*
Red-tailed vs. Ferruginous	0.1782 0.7446*	0.2133 0.7514*	0.1754 0.6787*
Swainson's vs. Random	−0.2739 0.0356	−0.2744 0.0196	−0.2701 0.0048
Red-tailed vs. Random	0.3840 0.8032*	0.3699 0.7681*	0.3367 0.7091*
Ferruginous vs. Random	−0.1372 0.4016	−0.1693 0.3426	−0.1435 0.3352

from Boise City or Keyes, the two largest towns in the county. All Ferruginous Hawk nests were >8 km from those towns, and all Red-tailed nests were >12 km distant. Four Swainson's Hawk nests were in "yards" ≤170 m from a house occupied occasionally (n = 1) or continually (n = 3). One Red-tailed Hawk nest was 40 m from an isolated, occupied house. Ten Swainson's Hawk nests were along major highways (<20 m from the road) in Cimarron County; no Ferruginous or Red-tailed hawk nests were similarly located.

We recorded tree species at 134 Swainson's, 31 Red-tailed, and 14 Ferruginous hawk nest sites. Most Swainson's Hawk nests were in Siberian elms, which were planted around homesteads in agricultural areas. Most Red-tailed Hawk nests occurred in riparian cottonwoods (Table 3).

DISCUSSION

Swainson's, Red-tailed, and Ferruginous hawks selected nest sites with different proportions of adjacent land cover types and topographic relief. Red-tailed and Ferruginous hawks nested almost exclusively in prairie. Red-tailed Hawks disproportionately used riparian timber surrounded by prairie for nesting. Ferruginous Hawks nested disproportionately in prairie and were more likely to use

TABLE 3. Number (%) of tree species used by *Buteos* in Cimarron County, Oklahoma, 2004–2005 (n = 179).

Tree species/nest substrate	Swainson's (n = 134)	Red-tailed (n = 31)	Ferruginous (n = 14)
Siberian elm (*Ulmus pumilla*)	95 (71.0)	1 (3.2)	5 (36.0)
Plains Cottonwood (*Populus deltoides*)	28 (21.0)	26 (84.0)	4 (29.0)
Red mulberry (*Morus rubra*)	4 (3.0)		
Hackberry (*Celtis occidentalis*)	3 (2.0)		
Osage orange (*Maclura pomifera*)	1 (0.7)		1 (7.0)
White mulberry (*Morus alba*)	1 (0.7)		
Oneseed juniper (*Juniperus monosperma*)	1 (0.7)		2 (14.0)
Black walnut (*Juglans nigra*)		1 (3.2)	
Honey locust (*Gleditsia triacanthos*)		1 (3.2)	1 (7.0)
Black locust (*Robinia pseudoacacia*)	1 (0.7)		
Artificial nest platform			1 (7.0)
Cliff		2 (6.5)	

areas with a high percentage of sandsage cover.

Swainson's Hawks were less selective in nesting habitat use than the other *Buteos*. They tended to use habitats in proportion to their availability and were the only *Buteo* nesting in agricultural areas. This is similar to the report by Bechard et al. (1990) in Washington, who also found Swainson's Hawk nests more likely to be associated with agriculture than either Ferruginous or Red-tailed hawks. Rothfels and Lein (1983) found Swainson's Hawks in agricultural areas and Red-tailed Hawks in the foothill parklands of the Rocky Mountains in Alberta.

Swainson's Hawks were more likely to nest near towns, occupied homes, and along highways in Cimarron County, and have been reported nesting in residential neighborhoods in California (England et al. 1995). Ferruginous Hawks are known to avoid human habitations (Olendorff 1993).

There was a potential sampling bias for finding higher numbers of Red-tailed Hawk nests than Swainson's Hawk nests along rivers, which could have reduced percent of prairie cover around Swainson's Hawk nests. Wooded floodplains of the Cimarron and Beaver rivers were frequently 0.50–0.75 km wide and examination of each tree was prohibitive. Red-tailed Hawks usually announced the presence of a nest with loud protests directed at the nest searcher, but Swainson's Hawks at times remained inconspicuous by sitting tight on a nest, even when the base of the nest tree was approached. We are confident that we located most, if not all, Red-tailed Hawk nests along the rivers investigated, but it is likely that at least some Swainson's Hawk nests were missed.

Cultivated areas in Cimarron County are flat, but prairie areas have more hills and cliffs. This may be a contributing factor to spatial partitioning of prairie and agricultural areas between Swainson's and Red-tailed hawks. Janes (1985) reported that Red-tailed Hawk nest sites had higher topographic relief and higher perch (telephone poles or trees ≥ 2 m tall) density, on average, than Swainson's Hawk nest sites. He attributed this to morphological differences which made Red-tailed Hawks more dependent on slope soaring and perch-hunting. Significant differences in topographic relief among *Buteo* nest sites in Cimarron County indicate these species may select habitats similar to those reported by Janes (1985). The higher mean maximum slope in buffers around Red-tailed Hawk nests supports the hypothesis that this species selected greater topographic relief relative to random sites (even random sites within prairie) or to habitats of the two congeners. We found two Red-tailed Hawk nests on cliffs in areas of extreme topographic relief, but no cliff-nesting Ferruginous or Swainson's hawks.

We did not quantify perch density around each nest, but significantly higher mean cover of wooded habitat around Red-tailed Hawk nests indicated a higher density of trees in their nesting areas. Most (83%) of the Red-tailed Hawk nests were along the Cimarron and Beaver rivers and associated drainages. Vast stretches of both rivers were heavily lined with cottonwoods and surrounded by prairie, enabling a hawk to access large tracts of prairie foraging areas from a constant supply of perch trees. Most Swainson's Hawk nests were in agricultural areas, where trees were more sparsely distributed and generally occurred as windbreaks around widely dispersed homesteads. The low number of natural perches in agricultural areas was augmented by utility poles, but they did not approach the density of perch trees along rivers.

We found species-specific differences in land cover around nest sites of Swainson's, Red-tailed, and Ferruginous hawks. These differences contributed to a pattern of spatial segregation of nest locations that may reduce interspecific competition in relatively homogeneous landscapes. We recognize that other landscape features around nests (e.g., fractal dimension, landscape diversity) may also be correlated with nest site choices with the species studied, but we focused on land cover and topography, which are the most readily available information for land managers to assess. Nest selection by Red-tailed and Ferruginous hawks in Cimarron County apparently occurs in advance of spring arrival of Swainson's Hawks. The potential interspecific nest site habitat partitioning among these species could be addressed in studies of diet overlap and nest productivity (e.g., Giovanni et al. 2007), and analyses of richness and habitat associa-

tions for *Buteo* prey species. Behavioral studies could examine the time allocation in each habitat type within a species' home range, which may be as important in identifying spatial habitat use as the specific nest location.

ACKNOWLEDGMENTS

Ranchers in Cimarron County graciously allowed access to their properties to conduct nest searches. John Shackford conducted field work with SM for both seasons of the project and located some of the raptor nests. Bill Voelker freely shared knowledge of Cimarron County raptors gained during almost 40 years of study in the area. Martin Piorkowski provided software expertise, Mark Payton provided statistical advice, and David Walter and Mahesh Rao provided GIS expertise. Financial support for this project was provided from State Wildlife Grants under Project T-4-P of the Oklahoma Department of Wildlife Conservation and Oklahoma State University administered through the Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma Department of Wildlife Conservation, Oklahoma State University, U.S. Geological Survey, U.S. Fish and Wildlife Service, and Wildlife Management Institute cooperating).

LITERATURE CITED

Andersen, D. E. and O. J. Rongstad. 1989. Home-range estimates of Red-tailed Hawks based on random and systematic relocations. Journal of Wildlife Management 53:802–807.

Bechard, M. J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. Condor 84:153–159.

Bechard, M. J. and J. K. Schmutz. 1995. Ferruginous Hawk (*Buteo regalis*). The birds of North America. Number 172.

Bechard, M. J., R. L. Knight, D. G. Smith, and R. E. Fitzner. 1990. Nest sites and habitats of sympatric hawks (*Buteo* spp.) in Washington. Journal of Field Ornithology 61:159–170.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. Available at http://www.spatialecology.com/htools

Cottrell, M. J. 1981. Resource partitioning and reproductive success of three species of hawks (*Buteo* spp.) in an Oregon prairie. Thesis. Oregon State University, Corvallis, USA.

England, A. S., J. A. Estep, and W. R. Holt. 1995. Nest-site selection and reproductive performance of urban-nesting Swainson's Hawks in the Central Valley of California. Journal of Raptor Research 29:179–186.

England, A. S., M. J. Bechard, and C. S. Houston. 1997. Swainson's Hawk (*Buteo swainsoni*). The birds of North America. Number 265.

Fisher, W. L. and M. S. Gregory. 2001. Oklahoma Gap Analysis Project: a geographic approach to planning for biological diversity. Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University, Stillwater, USA.

Gerstell, A. T. and J. C. Bednarz. 1999. Competition and patterns of resource use by two sympatric raptors. Condor 101:557–565.

Giovanni, M. D., C. W. Boal, and H. A. Whitlaw. 2007. Prey composition and provisioning by breeding Ferruginous Hawks and Swainson's Hawks on the southern Great Plains, USA. Wilson Journal of Ornithology 119:558–569.

Jaksic, F. M. and H. E. Braker. 1983. Food-niche relationships and guild structure in diurnal birds of prey: competition versus opportunism. Canadian Journal of Zoology 61:2230–2241.

Janes, S. W. 1985. Habitat selection in raptorial birds. Pages 159–188 *in* Habitat selection in birds (M. L. Cody, Editor). Academic Press, Orlando, Florida, USA.

Janes, S. W. 1994. Partial loss of Red-tailed Hawk territories to Swainson's Hawks: relations to habitat. Condor 96:52–57.

Leary, A. W., R. Mazaika, and M. J. Bechard. 1998. Factors affecting the size of Ferruginous Hawk home ranges. Wilson Bulletin 110:198–205.

Minitab Inc. 2000. Minitab statistical software. Release 13.20. Minitab Inc., State College, Pennsylvania, USA.

National Oceanic and Atmospheric Administration (NOAA). 2002. Climatography of the United States Number 81. Monthly station normals of temperature, precipitation, and heating and cooling degree days 1971–2000. www5.ncdc.noaa.gov/climatenormals/clim81/OKnorm.pdf (accessed 24 February 2006).

Oklahoma Department of Wildlife Conservation (ODWC). 2005. Oklahoma comprehensive wildlife conservation strategy. Oklahoma Department of Wildlife Conservation and Dynamic Solutions Inc. Report to the U.S. Fish and Wildlife Service. www.wildlifedepartment.com/CWCS.htm (accessed 23 February 2006).

Olendorff, R. R. 1993. Status, biology, and management of Ferruginous Hawks: a review. Special Report. Raptor Research and Technical Assistance Center, USDI, Bureau of Land Management, Boise, Idaho, USA.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Science 71:2141–2145.

Preston, C. R. and R. D. Beane. 1993. Red-tailed Hawk (*Buteo jamaicensis*). The birds of North America. Number 52.

Reinking, D. L. (Editor). 2004. Oklahoma Breeding Bird Atlas. University of Oklahoma Press, Norman, USA.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Iñigo-Elias, J. A. Kennedy, A. M. Martell, A. O. Panjabi, D. N. Pashley, K. V. Rosenberg, C. M. Rustay, J. S. Wendt, and T. C. Will.

2004. Partners in Flight North American landbird conservation plan. Cornell Laboratory of Ornithology, Ithaca, New York, USA.

RICKETTS, T. H., E. DINERSTEIN, D. M. OLSON, C. L. LOUCKS, W. EICHBAUM, D. DELLASALA, K. KAVANAGH, P. HEDAO, P. T. HURLEY, K. M. CARNEY, R. ABELL, AND S. WALTERS. 1999. Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington, D.C., USA.

ROTHFELS, M. AND M. R. LEIN. 1983. Territoriality in sympatric populations of Red-tailed and Swainson's hawks. Canadian Journal of Zoology 61:60–64.

SCHMUTZ, J. K., S. M. SCHMUTZ, AND D. A. BOAG. 1980. Coexistence of three species of hawks (*Buteo* spp.) in the prairie-parkland ecotone. Canadian Journal of Zoology 58:1075–1089.

TYRL, R. J., T. G. BIDWELL, AND R. E. MASTERS. 2002. Field guide to Oklahoma plants. Oklahoma State University, Stillwater, USA.

U.S. DEPARTMENT OF AGRICULTURE (USDA). 2003. National Agriculture Imagery Program. www2.ocgi.okstate.edu/2003img1 (accessed 22 November 2004).

U.S. DEPARTMENT OF AGRICULTURE (USDA). 2004. 2002 Census of agriculture, Oklahoma state and county data. www.nass.usda.gov/census/census02/volume1/ok/OKVolume104.pdf (accessed 24 February 2006).

U.S. GEOLOGICAL SURVEY (USGS). 2004. The National Map seamless server. seamless.usgs.gov/website/seamless/viewer.php (accessed 22 August 2005).

WOODBRIDGE, B. 1991. Habitat selection by nesting Swainson's Hawks: a hierarchical approach. Thesis. Oregon State University, Corvallis, USA.

The Wilson Journal of Ornithology 120(4):717–724, 2008

SPECIES RECOGNITION IN A VOCAL MIMIC: REPETITION PATTERN NOT THE ONLY CUE USED BY NORTHERN MOCKINGBIRDS IN DISCRIMINATING SONGS OF CONSPECIFICS AND BROWN THRASHERS

DUSTIN G. REICHARD[1,2,3] AND J. JORDAN PRICE[1]

ABSTRACT.—Vocal mimics that produce large repertoires of song types, such as in the Mimidae, have unique challenges discriminating songs of conspecifics from those of other mimids in areas where these species co-occur. We investigated cues used by Northern Mockingbirds (*Mimus polyglottos*) in discriminating their songs from songs of a sympatric mimid, the Brown Thrasher (*Toxostoma rufum*). We presented territorial mockingbirds with four playback treatments in which either mockingbird song types or thrasher song types had either a standardized mockingbird repetition pattern (5 repetitions) or a standardized thrasher pattern (2 repetitions). Four measures (time within 2 m of speaker, latency to approach, closest approach, and number of flights) were used to estimate a subject's response to each playback. Subjects responded significantly more strongly to mockingbird song types in a mockingbird repetition pattern than to thrasher song types in either repetition pattern. Responses to mockingbird song types in a thrasher repetition pattern elicited intermediate responses. Thus, mockingbirds can distinguish conspecific songs from Brown Thrasher songs based on song types alone regardless of their repetition pattern, although repetition pattern still appears to have a role in conspecific recognition. Brown Thrasher song includes a significantly broader frequency range than mockingbird song, which may allow direct discrimination. Our results suggest cues used by mimids in species discrimination are not necessarily the same as those used by human observers. *Received 29 October 2007. Accepted 23 April 2008.*

Discriminating songs of conspecifics from vocalizations of other species is fundamentally important for territorial songbirds. This discrimination in many species is facilitated by vocal features shared by individuals within a species but distinctive from sympatric species (reviewed in Becker 1982, Catchpole and Slater 1995, Marler 2004). The structure of many species' songs, despite variation across broad geographic ranges and even between neighboring conspecifics, is easily recognized by certain species-distinctive characteristics (e.g., Walton et al. 2002, Kroodsma 2005). Discrimination in songbirds that regularly mimic the sounds of other species is not as easy (Baylis 1982). Species discrimination is likely to be especially challenging between vocal mimics that produce large repertoires of song types, particularly when multiple mimicking species include imitations of the same sounds in their repertoires.

Northern Mockingbirds (*Mimus polyglottos*) and Brown Thrashers (*Toxostoma rufum*), Family Mimidae, provide an interesting illustration of the potential difficulties that different vocal mimics have in discriminating between each other's songs. Both species are highly versatile singers with large song repertoires (~100–400 song types/individual in mockingbirds: Wildenthal 1965; Merrit 1985; Derrickson 1987, 1988; >1,000 song types/individual in Brown Thrashers: Kroodsma and Parker 1977, Boughey and Thompson 1981), and repertoires of both species can include imitations of the same sounds (Boughey and Thompson 1976). Northern Mockingbirds and Brown Thrashers have widely overlapping geographic ranges in eastern North America, occupy many of the same habitats, and often sing during the same seasons and same times of day (Derrickson and Breitwisch 1992, Cavitt and Haas 2000). Both species defend territories, primarily against conspecifics, and there is little evidence that either species is interspecifically territorial towards the other (Howard 1974, Boughey and Thompson 1976, Cavitt and Haas 2000).

Ornithologists have long recognized that songs of Northern Mockingbirds and Brown Thrashers can be reliably distinguished in the field by their repetition patterns (e.g., Bent 1948, Walton et al. 2002). Mockingbirds typ-

[1] Department of Biology, St. Mary's College of Maryland, St. Mary's City, MD 20686, USA.

[2] Current address: Department of Biology, Indiana University, Bloomington, IN 47405, USA.

[3] Corresponding author; e-mail: dgreicha@indiana.edu

ically repeat each song type 4–5 times sequentially before producing the next song type in a sequence (range = 1–36 repetitions; Wildenthal 1965), whereas Brown Thrashers typically repeat each song type only twice in succession (range = 1–4 repetitions; Boughey and Thompson 1976). Whether these different repetition patterns are used by mockingbirds and thrashers in species discrimination is not clear. Boughey and Thompson (1976) showed that Brown Thrashers respond more strongly to normal thrasher song than to thrasher song altered to have a longer mockingbird-like repetition pattern, as measured by singing and approaches to a speaker. However, the same subjects did not respond differently to unaltered Brown Thrasher and mockingbird songs, which makes these results difficult to interpret. Responses of Northern Mockingbirds to similar manipulations of repetition pattern have not been previously reported.

We investigated cues used by Northern Mockingbirds, and specifically the importance of repetition pattern as a cue, in discriminating mockingbird songs from those of Brown Thrashers. A variety of vocal features other than number of song repetitions might differ consistently between these species and could be used by mockingbirds in conspecific recognition, including frequency and temporal characteristics of song types, intervals between sounds, song amplitude, or the presence of song types that are species-distinctive (Fletcher and Smith 1978, Baylis 1982, Becker 1982). We presented subjects with songs of both species in which song repetition patterns were manipulated but other aspects of songs, including sound amplitudes and a variety of temporal characteristics, were standardized. Our study tested whether mockingbirds preferentially use either song repetition patterns or characteristics of the song types in discriminating between species.

METHODS

Playback experiments were conducted from 25 September to 17 November 2006 on the campus of St. Mary's College of Maryland and the neighboring grounds of historic St. Mary's City, Maryland, USA (38° 11′ N, 76° 25′ W). The area includes abundant populations of both Northern Mockingbirds and Brown Thrashers, and members of both species defend territories in spring that can overlap interspecifically. Mockingbirds on our study site defend territories year-round and sing from mid-September through November as well as during the spring and summer, as reported for other mockingbird populations (Derrickson and Breitwisch 1992). Thrashers sing only during spring and most individuals leave the area during late fall (Hitchner 1996). We performed our study during fall when only mockingbirds were vocalizing and actively defending territories. This may have caused some of our playback treatments (e.g., those with Brown Thrasher songs) to seem unnatural, but it was unlikely to have influenced our subjects' abilities to discriminate songs of conspecifics from those of other species. Performing our experiments in fall also allowed us to minimize interference by Brown Thrashers during playback.

Songs of Northern Mockingbirds and Brown Thrashers were recorded in the field by the authors using a Marantz PMD 670 digital recorder and Telinga parabolic microphone or were obtained from the Macaulay Library of Natural Sounds (Cornell Laboratory of Ornithology, Ithaca, NY, USA) or other commercially available sources (Peterson 1990, Elliot et al. 1997). Song recordings used in the study (10 of mockingbirds and 7 of thrashers) were made in a variety of geographic locations and all were recorded in spring between March and July (Table 1). Mockingbirds produce repertoires of different song types in spring and in fall, and both repertoires have been shown to elicit agonistic responses in either season (Burnett 1978, Logan and Fulk 1984). We used spring songs because mockingbirds respond significantly more strongly to these vocalizations regardless of season (Logan and Fulk 1984).

We generated onscreen spectrograms for each recording (digitized at either 44.1 kHz or 48 kHz) using Audacity 1.2.4 software (Mazzoni et al. 2000) and selected 15 unique ~30-sec song sequences from each species based on recording quality. No more than three song sequences were taken from any one recorded individual. Each sequence in all cases included unique song types, and did not contain chats or begging calls. We altered song type repetition patterns to produce two versions of each song sequence (Fig. 1): one with a stan-

TABLE 1. Song recordings used in the study.

Species	Recording source
Mimus polyglottos	Peter P. Kellogg, Richmond Air Force Base, FL, May 1950
Mimus polyglottos	Robert C. Stein, Rock Springs, TX, April 1961
Mimus polyglottos	William W. Gunn, Homestead, FL, March 1968
Mimus polyglottos	Wilbur L. Hershberger, Frederick, MD, July 1997
Mimus polyglottos	Peterson (1990)
Mimus polyglottos	Elliot et al. (1997)
Mimus polyglottos	Authors, St. Mary's City, MD, April 2006
Mimus polyglottos	Authors, St. Mary's City, MD, April 2006
Mimus polyglottos	Authors, St. Mary's City, MD, April 2006
Mimus polyglottos	Authors, St. Mary's City, MD, April 2006
Toxostoma rufum	Geoffrey A. Keller, Ocala National Forest, FL, May 1994
Toxostoma rufum	Wilbur L. Hershberger, Frederick, MD, March 2000
Toxostoma rufum	Peterson (1990)
Toxostoma rufum	Elliot et al. (1997)
Toxostoma rufum	Authors, St. Mary's City, MD, April 2006
Toxostoma rufum	Authors, St. Inigoes, MD, May 2006
Toxostoma rufum	Authors, St. Inigoes, MD, May 2006

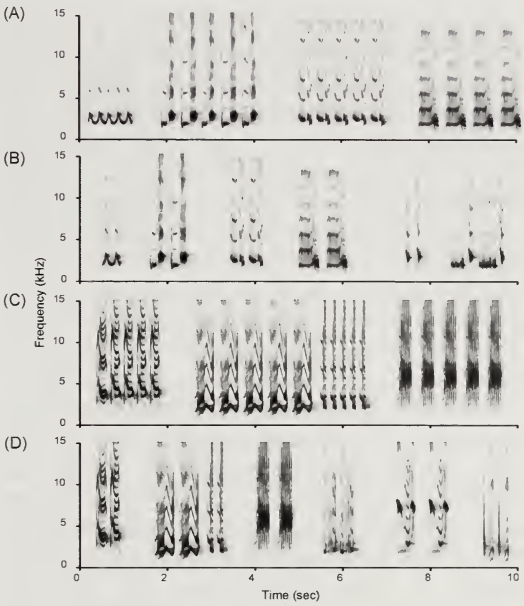


FIG. 1. Spectrograms of the four types of song sequences presented to Northern Mockingbird subjects: (A) mockingbird song types in a standardized mockingbird repetition pattern (5 repetitions), (B) mockingbird song types in a standardized Brown Thrasher pattern (2 repetitions), (C) thrasher song types in a mockingbird pattern, and (D) thrasher song types in a thrasher pattern.

dardized mockingbird pattern (5 repetitions/bout) and one with a standardized thrasher pattern (2 repetitions/bout). We follow Derrickson and Breitwisch (1992) in defining a "song type" as an acoustically distinct sound pattern, usually repeated more than once sequentially, and in defining a "bout" as a group of repeated song types. Intervals between song types and between bouts were not altered in these manipulations, and sounds that were not repeated in these recordings (short sounds that occurred in <25% of recordings) were deleted. All recordings were passed through a 10-band equalizer to remove low frequency background noise below 320 Hz and normalized to the same peak amplitude using Sound Studio 2.2.4 (Freeverse Inc., New York, NY, USA). Each song sequence used in playback experiments was repeated several times sequentially for a total playback duration of 3 min (mean ± SE number of song types/playback: NM = 14.2 ± 0.9, BT = 18.6 ± 0.9; mean ± SE number of bouts/3 min playback: NM/NM = 73.5 ± 5.6, NM/BT = 136.7 ± 9.4, BT/BT = 128.9 ± 5.6, BT/NM = 66.9 ± 3.5). Each initial recording was used to create two treatment stimuli, one for each repetition pattern type, but both variations from the same original recording were not played to the same subject. Precautions were also taken to ensure that subjects would not hear their own songs or the songs of a nearby neighbor. Thus, each subject heard four song sequences with different song types.

Fifteen territorial mockingbird subjects were each presented with four different treatments: (1) Northern Mockingbird song types in a standardized mockingbird repetition pattern (NM/NM), (2) mockingbird song types in a standardized Brown Thrasher repetition pattern (NM/BT), (3) thrasher song types in a standardized mockingbird repetition pattern (BT/NM), and (4) thrasher song types in a standardized thrasher repetition pattern (BT/BT). Treatments for each subject were presented in random order on the same day at

different locations in the territory, separated by a minimum of 15 min of silence to minimize habituation and fatigue. The speaker was relocated during these intervals within the subject's territory for the next treatment. Small shrubs and trees with similar branch densities were chosen for each speaker location, and speaker locations were approximately equidistant from one another as well as from estimated territorial boundaries to control for speaker movement. Territorial boundaries were estimated by a non-invasive observation period of 15–30 min the day before playback was performed. Researchers measuring the responses of subjects did not know the order in which treatments were presented at the time of playback to minimize observer bias, although the repetition pattern was likely discernable after the first few song types were heard.

Each treatment began only when the bird was visible, and a trial (playback of all 4 treatments) was aborted if the subject was lost from view for >15 min. Birds were not color banded for individual identification in our study; however, subjects were followed visually throughout each trial to ensure the same individual was observed in all four treatments. Males and females are visually indistinguishable in mockingbirds, and females are known to sing occasionally during fall (Derrickson and Breitwisch 1992). We attempted to focus on males by identifying them by their more frequent singing behaviors before each experiment. Songs were broadcast using an SME-AFS amplified field speaker (Saul Mineroff Electronics Inc., Elmont, NY, USA) connected to a 6 GB iPod Mini (Apple Inc., Cupertino, CA, USA). We standardized the volume of playback using a Realistic digital sound pressure level meter (fast response, C weighting) to approximate that of naturally singing birds. All experiments were conducted during the period of highest bird activity between 0700 and 1030 hrs EST and only under favorable weather conditions.

We measured responses of subjects during each 3-min playback period by recording four measures: (1) the amount of time, in seconds, each bird spent within 2 m of the speaker, (2) the latency, in seconds, to approach towards the speaker >1 m after playback began, (3) the closest approach to the speaker, and (4) the number of flights >1 m. We conducted a principal components analysis using these four behavioral response measures as variables to assess the overall strength of response to each treatment. The response measures loaded about equally on the first principal component (Table 2), which explained 64.5% of the total variation. We analyzed the resulting response scores (PC I) with a one-way ANOVA and a Tukey's HSD post hoc test to compare responses between the four treatments. We also compared each response measure individually between treatments using a one-way repeated measures ANOVA with a Bonferroni post hoc test.

TABLE 2. Loadings of individual response measures on the first principal component for playback treatments.

Response measure	Loading score
Time within 2 m of speaker	−0.769
Latency to approach	0.827
Closest approach to speaker	0.894
Number of flights	−0.711

We analyzed the song sequences used in playback following these experiments to investigate the possibility that our treatments differed in aspects other than song type repetition pattern. We measured mean song type durations, bout durations, intervals between bouts, and song type repetition rates for each song sequence used in playback using Raven, Version 1.2.1 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Five bouts were chosen randomly from each recording for these measurements, which were used to calculate a mean measurement for each song sequence. We also measured the highest and lowest peak frequencies ("maximum frequency" in spectrogram slices in Raven) that occurred in each song sequence to calculate the range of frequencies used (following Price et al. 2006). These data were analyzed using a two sample F-test for variances and an independent measures t-test.

RESULTS

A principal components analysis including time spent within 2 m of the speaker, latency to approach, closest approach, and number of flights (Fig. 2A) revealed significantly differ-

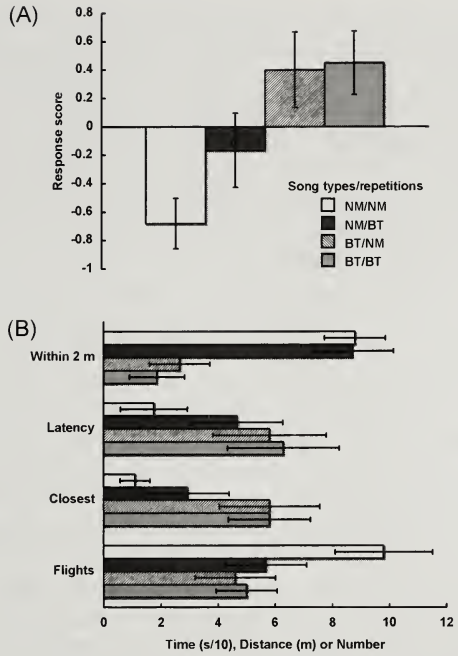


FIG. 2. (A) Mean (±SE) scores from a principal components analysis of mockingbird responses to playback treatments in which either Northern Mockingbird (NM) or Brown Thrasher (BT) song types were presented in either a NM or BT repetition pattern. (B) Mean (±SE) response measures included in the principal components analysis: time spent within 2 m of the speaker (Within 2 m), latency to approach >1 m towards the speaker (Latency), closest approach to the speaker (Closest), and number of flights (Flights) (n = 15 subjects).

ent responses to mockingbird song types in a mockingbird repetition pattern (NM/NM) than to Brown Thrasher song types with either repetition pattern (one-way ANOVA with Tukey's HSD post hoc, n = 15, $F_{3,56}$ = 5.177; BT/BT, P = 0.006; BT/NM, P = 0.01). Birds responded similarly to Brown Thrasher song types regardless of repetition pattern (P > 0.99). Mockingbird song types in a thrasher repetition pattern (NM/BT) elicited an intermediate response that was not significantly different from responses to any of the other three treatments (BT/BT, P = 0.26; BT/NM, P = 0.33; NM/NM, P = 0.41).

Mockingbirds generally responded more strongly to playback of conspecific song types than to Brown Thrasher song types, comparing individual response measures among treatments (Fig. 2B). For example, subjects spent significantly more time within 2 m of the speaker during both treatments with mockingbird song types than during treatments with Brown Thrasher song types (one-way repeated measures ANOVA with Bonferroni post hoc, $F_{3,42}$ = 13.328, NM/NM vs. BT/BT, P = 0.001; NM/NM vs. BT/NM, P = 0.002; NM/BT vs. BT/BT, P = 0.011; NM/BT vs. BT/NM, P = 0.048). Responses to the same song types with different repetition patterns did not differ in time spent near the speaker (NM/NM vs. NM/BT, P > 0.99; BT/BT vs. BT/NM, P > 0.99). Latency to approach did not differ significantly among treatments ($F_{3,42}$ = 2.106, P = 0.13); however, 13 of 15 subjects responded in 10 sec or less to NM/NM songs, whereas only 7 of 15 responded as quickly during NM/BT songs and 6 of 15 during both BT/NM and BT/BT treatments. Subjects approached the speaker somewhat more closely during NM/NM playback than during treatments with BT/BT songs ($F_{3,42}$ = 2.997, P = 0.03) or BT/NM songs (P = 0.098). Subjects also performed significantly more flights in response to NM/NM songs than to Brown Thrasher song types with either repetition pattern ($F_{3,42}$ = 5.773; BT/BT, P = 0.031; BT/NM, P = 0.029). No behavioral measures differed significantly in response to the two treatments with Brown Thrasher song types (BT/NM and BT/BT).

Measurements of the song sequences used in our playback experiments revealed no significant differences in mean song type durations between Northern Mockingbirds and Brown Thrashers (t-test: two sample assuming unequal variances, n = 15, P = 0.28). There was no significant difference in bout duration between treatments with the same repetition pattern (P = 0.88), but bout duration was significantly different between treatments with two repetitions/song type and five repetitions/song type (P = 0.003). We found no differences in the mean intervals between bouts with different repetition patterns (P = 0.61). Songs with different song types but the same repetition patterns did not differ in their mean song repetition rates (NM/NM vs. BT/NM, P = 0.48; NM/BT vs. BT/BT, P = 0.32) or in the total number of bouts included in each playback (NM/NM vs. BT/NM, P = 0.48; NM/BT vs. BT/BT, P = 0.32). Songs with mockingbird song types, however, exhibited a

significantly narrower range of mean peak frequencies (800–6,700 Hz) than songs with thrasher song types (600–9,250 Hz; $P < 0.001$). Brown Thrasher songs included both significantly lower frequencies ($P = 0.008$) and significantly higher frequencies ($P < 0.001$) than mockingbird songs, on average, which may be attributed to more energy in the upper harmonics of thrasher song (Fig. 1).

DISCUSSION

Our results indicate that Northern Mockingbirds can distinguish between conspecifics and Brown Thrashers based on their song types alone, regardless of the repetition pattern in which these songs are presented. Subjects responded strongly to playback of mockingbird song types in a standardized mockingbird repetition pattern, but responded relatively little to Brown Thrasher song types even when these sounds were played in exactly the same pattern of five repetitions/bout. Mockingbird song types with a Brown Thrasher repetition pattern elicited intermediate responses, generally stronger than responses to Brown Thrasher song types but not as strong as the responses to normal mockingbird song. Thus, although repetition pattern was not the principal cue used by our subjects to discriminate their own species' songs from thrasher songs, it appeared to have a role in conspecific recognition.

Most North American field guides indicate that songs of species in Family Mimidae (e.g., Northern Mockingbirds, Brown Thrashers, Gray Catbirds [*Dumetella carolinensis*]) can be most easily distinguished by their distinctive repetition patterns (e.g., Bent 1948, Cimprich and Moore 1995, Cavitt and Haas 2000, Walton et al. 2002); this cue is widely used by human observers in recognizing songs of these three species. Our results are surprising in demonstrating that mockingbirds preferentially use different vocal cues than what we typically use in discriminating species. None of our playback songs differed consistently in song type durations, amplitudes, or in intervals between song types or bouts. Our subjects appeared to recognize conspecific vocalizations based on acoustic features of the song types themselves.

Mockingbirds apparently have the ability to distinguish between two and five items, based on a study by Farnsworth and Smolinski (2006) which focused on visual discrimination. In mockingbird song, however, the number of times in which song types are repeated can potentially vary over a relatively wide range (1–36 times according to Wildenthal 1965), which could explain in part why repetition pattern is not used as a primary cue in conspecific recognition.

Northern Mockingbirds increase the number of repetitions/bout during countersinging between territorial males (Derrickson 1988). Experiments with a closely related species, Tropical Mockingbird (*Mimus gilvus*), show that territorial males respond more strongly to a higher number of repetitions/bout during playback (Botero and Vehrencamp 2007). Playing mockingbird song types with a higher number of repetitions in our study elicited a stronger response, but increasing the repetition number of thrasher song types had no measurable effect on mockingbird responses. Repetition pattern in mockingbirds might have an important role in communication between territorial males rather than simply advertising species or individual identity. Mockingbirds are also known to decrease repetitions/bout during courtship and intersexual singing (Derrickson 1988). It is possible that our treatment of only two repetitions/bout was recognized as a mockingbird repetition pattern, although one atypical for the season. This may explain the intermediate response of our subjects to this treatment.

Our findings agree somewhat with results of previous playback studies in which other mimid species were tested using songs with artificially altered patterns (Boughey and Thompson 1976, Fletcher and Smith 1978). For example, Gray Catbirds apparently do not distinguish their songs from those of other mimids based on repetition pattern alone. Altering repetition patterns of catbird, thrasher, or mockingbird songs has no apparent effect on a catbird's ability to recognize species (Boughey and Thompson 1976); changing the order of catbird song types or even playing their songs backwards also has no effect (Fletcher and Smith 1978). Boughey and Thompson (1976) demonstrated that Brown Thrashers respond similarly to mockingbird song types with different repetition rates, including a thrasher-like repetition pattern.

Brown Thrashers respond more strongly to Brown Thrasher songs in the normal repetition pattern than to thrasher songs in a mockingbird pattern, suggesting that repetition pattern is important for species recognition in thrashers. However, these experiments also showed that Brown Thrashers do not discriminate between normal conspecific song and normal mockingbird song, which makes these results difficult to interpret.

How our mockingbird subjects were able to distinguish mockingbird song types from Brown Thrasher song types with the same repetition pattern is not clear. One possibility is that our subjects were familiar with song types we included in the study or that mockingbird songs generally include song types that are species-specific and indicate species identity. This seems unlikely, however, as most of our subjects appeared to make this discrimination after hearing only a few different song types (i.e., within the first 10 sec of playback). Furthermore, mockingbirds include an extensive variety of mimicked sounds in their song repertoires (Derrickson and Breitwisch 1992) and composition of these repertoires can vary geographically (Thompson et al. 2000), with age and social context (Derrickson 1987, 1988), and even seasonally between spring and fall (Burnett 1978). Our study was conducted in fall and included mockingbird songs recorded in spring from widely different locations and different years (Table 1). Some songs used in our study had been recorded from birds in our study population (4 Northern Mockingbird songs and 1 Brown Thrasher song), but we made sure that subjects did not hear their own song types or song types recorded from a nearby territory.

A more likely explanation for our results is that mockingbird and Brown Thrasher song types differ consistently in certain acoustic characteristics. We found that Brown Thrashers use a significantly wider range of sound frequencies than mockingbirds, as has been noted in previous studies (Wildenthal 1965, Boughey and Thompson 1976; Fig. 1). It is possible that mockingbirds are unable to produce the extremely high and low frequency whistles of which Brown Thrashers are capable, and studies investigating the limitations on song performance in mockingbirds are consistent with this possibility (*ca.* 750 Hz – *ca.* 7,000 Hz in Zollinger and Suthers 2004). Other attributes that might differ between these species, not investigated in our study, include rate and pattern of frequency changes within song types, production of two sounds simultaneously, relative amplitudes of harmonics, and overall song amplitude. Further studies will be needed to identify the principal cues used by these birds and by other vocal mimics in recognizing conspecifics by song.

ACKNOWLEDGMENTS

We thank Megan Stallman, Mary Clapp, Cathy Brandt, Emily Myron, and Katie Zdilla for assistance in the field, and Kevin Boyle for help in developing the project and field assistance. We also thank Dawn O'Neal, Sara Schrock, Amy Skypala, and four anonymous reviewers for comments on the manuscript. Funding for this study was provided by a grant from the Maryland Ornithological Society and a Myron Marlay Award from St. Mary's College of Maryland to D. G. Reichard.

LITERATURE CITED

Baylis, J. R. 1982. Avian vocal mimicry: it's function and evolution. Pages 51–83 *in* Acoustic communication in birds. Volume 2 (D. E. Kroodsma and E. H. Miller, Editors). Academic Press, New York, USA.

Becker, P. H. 1982. The coding of species-specific characteristics in bird sounds evolution. Pages 213–252 *in* Acoustic communication in birds. Volume 1 (D. E. Kroodsma and E. H. Miller, Editors). Academic Press, New York, USA.

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. National Museum Bulletin. Number 195.

Botero, C. A. and S. L. Vehrencamp. 2007. Responses of male Tropical Mockingbirds (*Mimus gilvus*) to variation in within-song and between-song versatility. Auk 124:185–196.

Boughey, M. J. and N. S. Thompson. 1976. Species specificity and individual variation in the songs of the Brown Thrasher (*Toxostoma rufum*) and Catbird (*Dumetella caroliuensis*). Behaviour 57:64–90.

Boughey, M. J. and N. S. Thompson. 1981. Song variety in the Brown Thrasher (*Toxostoma rufum*). Zeitschrift für Tierpsychologie 56:47–58.

Burnett, L. J. 1978. Mockingbird song (*Mimus polyglottos*): an investigation within and across seasons. Thesis. University of North Carolina, Greensboro, USA.

Catchpole, C. K. and P. J. B. Slater. 1995. Bird song: biological themes and variations. Cambridge University Press, New York, USA.

Cavitt, J. F. and C. A. Haas. 2000. Brown Thrasher (*Toxostoma rufum*). The birds of North America. Number 557.

CIMPRICH, D. A. AND F. R. MOORE. 1995. Gray Catbird (*Dumetella carolinensis*). The birds of North America. Number 167.

DERRICKSON, K. C. 1987. Yearly and situational changes in the estimate of repertoire size in Northern Mockingbirds (*Mimus polyglottos*). Auk 104:198–207.

DERRICKSON, K. C. 1988. Variation in repertoire presentation in Northern Mockingbirds. Condor 90: 592–606.

DERRICKSON, K. C. AND R. BREITWISCH. 1992. Northern Mockingbird (*Mimus polyglottos*). The birds of North America. Number 7.

ELLIOT, L., D. STOKES, AND L. STOKES. 1997. Stokes field guide to bird songs, eastern region. Time Warner Audiobooks, New York, USA.

FARNSWORTH, G. L. AND J. L. SMOLINSKI. 2006. Numerical discrimination by wild Northern Mockingbirds. Condor 108:953–957.

FLETCHER, L. E. AND D. G. SMITH. 1978. Some parameters of song important in conspecific recognition by Gray Catbirds. Auk 95:338–347.

HITCHNER, S. 1996. Brown Thrasher. Pages 298–299 *in* Atlas of the breeding birds of Maryland and the District of Columbia (C. S. Robbins, Editor). University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.

HOWARD, R. D. 1974. The influence of sexual selection and interspecific competition on Mockingbird song (*Mimus polyglottos*). Evolution 28:428–438.

KROODSMA, D. E. 2005. The singing life of birds: the art and science of listening to birdsong. Houghton Mifflin Company, Boston, Massachusetts, USA.

KROODSMA, D. E. AND L. D. PARKER. 1977. Vocal virtuosity in the Brown Thrasher. Auk 94:783–785.

LOGAN, C. A. AND K. R. FULK. 1984. Differential responding to spring and fall song in Mockingbirds (*Mimus polyglottos*). Journal of Comparative Psychology 98:3–9.

MARLER, P. 2004. Science and birdsong: the good old days. Pages 11–18 *in* Nature's music (P. Marler and H. Slabbekoorn, Editors). Elsevier Academic Press, New York, USA.

MAZZONI, D., M. BRUBECK, J. CROOK, V. JOHNSON, L. LUCIUS, AND M. MEYER. 2000. Audacity, Version 1.2.4. SourceForge.net, Fremont, California, USA.

MERRIT, P. G. 1985. Song function and the evolution of song repertoires in the Northern Mockingbird (*Mimus polyglottos*). Dissertation. University of Miami, Coral Gables, USA.

PETERSON, R. T. 1990. A field guide to bird songs: eastern and central North America. Third Edition. Houghton Mifflin Company, Boston, Massachusetts, USA.

PRICE, J. J., S. M. EARNSHAW, AND M. S. WEBSTER. 2006. Montezuma Oropendolas modify a component of song constrained by body size during vocal contests. Animal Behaviour 71:799–807.

THOMPSON, N. S., E. ABBY, J. WAPNER, C. LOGAN, P. G. MERRITT, AND A. POOTH. 2000. Variation in the bout structure of Northern Mockingbird (*Mimus polyglottos*) singing. Bird Behavior 13:93–98.

WALTON, R. K., R. W. LAWSON, AND R. T. PETERSON. 2002. Birding by ear: eastern and central North America. Houghton Mifflin Company, Boston, Massachusetts, USA.

WILDENTHAL, J. L. 1965. Structure in primary song of the Mockingbird (*Mimus polyglottos*). Auk 82: 161–189.

ZOLLINGER, S. A. AND R. A. SUTHERS. 2004. Motor mechanisms of a vocal mimic: implications for birdsong production. Proceedings of the Royal Society of London Series B Biological Sciences 271: 483–491.

The Wilson Journal of Ornithology 120(4):725–731, 2008

LESSER SNOW GEESE AND ROSS'S GEESE FORM MIXED FLOCKS DURING WINTER BUT DIFFER IN FAMILY MAINTENANCE AND SOCIAL STATUS

JÓN EINAR JÓNSSON[1,2,4] AND ALAN D. AFTON[3]

ABSTRACT.—Smaller species are less likely to maintain families (or other forms of social groups) than larger species and are more likely to be displaced in competition with larger species. We observed mixed-species flocks of geese in southwest Louisiana and compared frequencies of social groups and success in social encounters of Lesser Snow Geese (*Chen caerulescens caerulescens*; hereafter Snow Geese) with that of the smaller, closely-related Ross's Geese (*C. rossii*). Less than 7% of adult and <4% of juvenile Ross's Geese were in families, whereas 10–22% of adult and 12–15% of juvenile Snow Geese were in families. Snow Geese won 70% of interspecific social encounters and had higher odds of success against Ross's Geese than against individuals of their own species. The larger Snow Geese maintain families longer than Ross's Geese, which probably contributes to their dominance over Ross's Geese during winter. Predator vigilance probably is an important benefit of mixed flocking for both species. We suggest the long-standing association with Snow Geese (along with associated subordinate social status) has selected against family maintenance in Ross's Geese. *Received 23 August 2007. Accepted 27 February 2008.*

Body size seemingly influences social behavior and foraging behavior in many animals (Calder 1996). Body size has important physiological implications for birds: (1) rate of heat loss increases with decreasing body size because of increasing surface to volume ratio (Goudie and Ankney 1986, Calder 1996); (2) mass-specific metabolic rate is inversely related to body mass (Kendeigh 1970, Calder 1996); (3) gut size scales linearly with body size and partly affects the rate of energy extraction from food (Demment and Van Soest 1985); and (4) larger species generally have greater fasting endurances than smaller species (Goudie and Ankney 1986, Calder 1996, Jónsson et al. 2007). Smaller species are relatively less likely to maintain social groups, generally select more sheltered habitats, and consume more specialized diets (Jarman 1974, Shelley et al. 2004). Smaller species also are more likely to be displaced in competition with larger species, regardless of numbers present (Shelley et al. 2004) and often use scramble tactics in competition for food (Krause and Ruxton 2002). Smaller species generally are more vulnerable to predator attacks than larger species, but can benefit by forming mixed flocks with larger species, which at times have better predator detection capabilities (McWilliams et al. 1994, Kristiansen et al. 2000, Randler 2004).

Most geese, including Lesser Snow Geese (*Chen caerulescens caerulescens*; hereafter Snow Geese) maintain families from one breeding season to the beginning of the next (family social system) (Boyd 1953; Raveling 1970; Prevett and MacInnes 1980; Black and Owen 1989a, b; Gregoire and Ankney 1990; Kalmbach 2006). Larger goose families generally are dominant over smaller families, pairs, and lone geese (Loonen et al. 1999, Stahl et al. 2001, Kalmbach 2006). Parents apparently profit from juvenile assistance when defending patches of food from other flock members (contributor effect hypothesis, Black and Owen 1989b).

Conversely, smaller goose species may not maintain families in winter (McWilliams and Raveling 1998). In California, Ross's Geese (*C. rossii*) form denser flocks than larger goose species when foraging on grasslands where they often associate with Cackling Geese (*Branta hutchinsii*) (Johnson and Raveling 1988, McWilliams and Raveling 1998). Only a small percentage of Ross's Geese in California are paired or in families (dense-flock social system) (Johnson and Raveling

[1] School of Renewable Natural Resources, Louisiana State University, Baton Rouge, LA 70803, USA.

[2] Current address: University of Iceland, Snæfellsnes Research Centre, Hafnargata 3, 340 Stykkishólmur, Iceland.

[3] USGS, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge, LA 70803, USA.

[4] Corresponding author: e-mail: joneinar@hi.is

1988, McWilliams and Raveling 1998). Family maintenance varies in relation to food choices (seeds vs. leafs and tubers) and fine-scale spatial distribution of selected food plants among habitats (McWilliams and Raveling 1998).

Ross's Geese probably are more at risk from avian predators than are larger goose species and predation pressure may have been an important evolutionary factor (albeit not the only factor) influencing their social system during winter (McWilliams et al. 1994). In addition, denser flocks may convey benefits of decreased nearest neighbor distance, i.e., birds in denser flocks are able to spend more time feeding and less time vigilant (Fernandez-Juricic et al. 2004, 2007).

Southwest Louisiana is a historical wintering area for Snow Geese (Jónsson and Afton 2006 and citations therein), but Ross's Geese only began wintering in Louisiana during the last decade (Jónsson 2005). Ross's Geese in Louisiana occur only in rice-prairies (cultivated former tall-grass prairie) where they primarily forage in rice fields in mixed flocks with Snow Geese. Ross's Geese have small bills that are adapted for grazing on grass (Ryder and Alisauskas 1995). Thus, they are rarely found in marshes along the Gulf Coast, which are historical habitats of Snow Geese (which have larger bills adapted for excavation of marsh plants) (Alisauskas 1998).

Dominant goose species can affect feeding behavior, distribution, and food selection of less aggressive species when feeding in mixed flocks (Kristiansen and Jarrett 2002). Interspecific dominance relationships often are affected by the number of individuals present from each species (i.e., the more numerous species is dominant within mixed flocks; Fox and Madsen 1981, Madsen 1985, Gawlik 1994), although exceptions are known (Kristiansen and Jarrett 2002).

We present the first quantitative comparison of (1) frequencies of pairs and families, and (2) frequencies and outcomes of intra- and interspecific social encounters of Ross's Geese and Snow Geese in mixed wintering flocks. Our study provides a comparison of two closely-related species of varying size foraging together on the same plant species and controls for effects of macro habitat, geographical location, season, and climate (Jónsson et al. 2007).

METHODS

Study Area.—We observed Snow Geese and Ross's Geese in the rice prairie region of southwest Louisiana in winters 2002–2003 and 2003–2004 (Jónsson 2005; Jónsson and Afton 2006, 2008). Rice prairies are former tall-grass prairies which are extensively cultivated and managed, mostly for rice, but also as pasture for cattle (Alisauskas et al. 1988, Bateman et al. 1988). This area has been described by Alisauskas et al. (1988) and Bateman et al. (1988).

We exclusively observed mixed flocks comprised of Snow Geese and Ross's Geese using foraging habitats, i.e., non-flooded ricefields, which were uncut, stubble, tilled, or fallow (Alisauskas et al. 1988, Jónsson 2005). Ross's Geese comprised, on average, 7% of observed mixed white goose flocks during our study. Estimated combined Snow Goose and Ross's Goose numbers on our study area were 257,119 in 2002–2003 and 360,487 in 2003–2004 (Fronczak 2004).

Sampling of Focal Geese.—Three trained observers and JEJ collected behavioral data in winters 2002–2003 and 2003–2004; JEJ was the only observer present in both winters and trained other observers, until results of observation of the same focal birds were nearly identical among observers (Jónsson and Afton 2006, 2008). We are confident that inter-observer variation between or within years did not bias our results.

We sampled goose behavior 3-4 days/week from 10 November until 10 February each winter. Observations were made during daylight between 0800 and 1700 hrs CST. Mixed flocks were large (a few hundred to a few thousand), mobile, and flushed often; thus, risk of repeated sampling of individuals was minimal.

Observers used 20× spotting scopes and collected 5 to 10-min focal sampling observations of randomly selected individuals (Altmann 1974). We used sequences of 20 random numbers to select focal geese within a field of vision, counting from left or right until a goose was located that corresponded to each random number.

Time of day was not a variable of biological

interest in this study. We attempted *a priori* to control for time of day variation in behavior by alternating between species during field observations to ensure that comparisons between species were unbiased (Jónsson and Afton 2006, 2008). Both species were sampled equally during mid-day (1100–1300 hrs) when geese were relatively prone to cease activities and rest.

We assigned age classes to Snow Geese and Ross's Geese based on plumage color and patterns (Ryder and Alisauskas 1995, Mowbray et al. 2000). We assigned pair and family status to individuals under observation based on mutual participation in social encounters, mutual chasing or avoiding other geese, and coordinated directions of locomotion (Raveling 1970, Black and Owen 1989a, Gregoire and Ankney 1990). We categorized focal individuals into five social groups (after Boyd 1953, Raveling 1970, Gregoire and Ankney 1990): (1) *lone adult*, a lone after-hatch-year goose; (2) *parent*, adult goose bonded (i.e., paired) with another adult goose, accompanied by at least one hatch-year bird; (3) *paired non-parent*, adult goose bonded with another adult goose without hatch-year birds; (4) *juvenile in family*, hatch-year goose accompanied by adult parents; and (5) *lone juvenile*, a lone hatch-year goose.

We recorded frequencies of social encounters between focal geese and other geese, scoring wins if opponents responded to interactions by avoiding or fleeing focal geese; focal birds were assigned a loss if an opponent chased them (Raveling 1970, Gregoire and Ankney 1990). We only recorded social encounters directly involving focal geese, their mates, parents or offspring.

Statistical Analyses.—We used a generalized linear model in PROC GENMOD (Agresti 1996, SAS Institute 1999) to estimate whether frequencies of social groups (parents, non-parental pairs, and lone geese) differed between species, age groups, and winters, which were categorical explanatory variables. Final models were selected using backwards stepwise model selection (Agresti 1996), except the age × social group interaction was fixed (regardless of significance) in this model because pairs without juveniles were not observed in the juvenile category.

We constructed generalized linear models based on normal and Poisson distributions; the Poisson log-linear model is equivalent to a logistic regression based on the multinomial distribution (Agresti 1996). We evaluated goodness of fit for these models by comparing ratios between degrees of freedom (df) and deviance of the models; a ratio of deviance/df close to 1.0 indicates a good model fit (Agresti 1996). A linear model based on the normal distribution fit the data reasonably well (deviance = 24.0, df = 15), whereas the Poisson model gave a poorer fit (deviance = 149.6, df = 15).

We calculated probabilities of winning encounters against the other species (P_{other}) and compared odds of success ($O_{success}$) in interspecific social encounters versus intraspecific social encounters for both species. Our goal was to quantify success in interspecific encounters, using success in intraspecific encounters as a baseline value. We calculated odds ratios of winning against the other species over the odds of winning against a conspecific (O_{own}) as:

$$\{O_{success} \text{ against other species} = \text{Probability of winning } (P_{other})/(1 - P_{other})\} \div \{O_{success} \text{ against own species} = \text{Probability of winning } (P_{own})/(1 - P_{own})\}.$$

We assumed that differing odds of success (unequal odds ratio) between Snow Geese and Ross's Geese indicated that one species was dominant over the other species, whereas odds ratios of ~1 indicated equal success in interspecific social encounters and equal social status for the species.

RESULTS

Frequencies of social groups differed between species ($\chi^2 = 6.12$, $P = 0.013$) and age groups ($\chi^2 = 35.55$, $P < 0.001$), but not between winters ($\chi^2 = 0.53$, $P = 0.466$). The ratio of juveniles to adults was relatively higher for Snow Geese in both winters (Table 1). Less than 7% of adult and <4% of juvenile Ross's Geese were in families, whereas 10–22% of adult and 12–15% of juvenile Snow Geese were in families (Table 1).

On average, focal Snow Geese were three to 10 times more likely to have intraspecific encounters than interspecific encounters (Ta-

TABLE 1. Age and social groups (% of observations) of focal Lesser Snow Geese and Ross's Geese in the rice prairies of southwest Louisiana during winters, 2002–2003 and 2003–2004.

		Lesser Snow Geese		Ross's Geese	
Age	Social group	2002–2003	2003–2004	2002–2003	2003–2004
Adults	Lone	40.5	31.1	58.9	40.7
	Paired parents	9.8	22.1	0.0	6.9
	Paired non-parents	26.0	25.4	29.5	41.6
Juveniles	Lone	11.7	6.7	11.3	7.2
	In a family	12.1	14.7	0.3	3.6
	Age ratio[a]	23.8	21.4	11.6	10.8
	N[b]	405	302	319	305

[a] Percent juveniles within *N*.
[b] Number of focal individuals.

ble 2). In contrast, focal Ross's Geese engaged in intra- and interspecific social encounters with equal frequency in 2003–2004, but had 3 times more interspecific social encounters than intraspecific social encounters in 2002–2003 (Table 2). Focal Snow Geese were more likely to win social encounters with Ross's Geese than with other Snow Geese (Table 2). Focal Snow Geese were relatively more successful in interspecific social encounters; Snow Geese won 30 of 52 social encounters in 2002–2003, and 32 of 33 social encounters in 2003–2004 (Table 2). Snow Geese won 63 of 87 (72.4%) interspecific social encounters observed when all focal observations of both species were combined. Focal birds of both species were more successful in intraspecific social encounters in 2003–2004 than in 2002–2003 (Table 2).

Overall, focal Snow Geese lost only 10 social encounters against Ross's Geese; all Ross's Goose wins were against lower ranked Snow Geese (i.e., non-parental pairs and lone birds); six were against lone juvenile Snow Geese, three were against lone adult Snow Geese, and one win was against an adult pair. Focal Ross's Geese did not win social encounters against Snow Geese in families.

DISCUSSION

Family Maintenance.—Our data from Louisiana, combined with that from other locations, indicate Ross's Geese maintain families for shorter periods than Snow Geese throughout their current wintering ranges. Timing of family break-up is known to vary among species, individuals, and years (Prevett and MacInnes 1980, Black et al. 2007). Eighty percent of all juvenile Snow Geese wintering in the Mississippi Flyway are in families from 20 December to 15 March, whereas <50% of all goslings are in families on staging areas in late March and early April (Prevett and MacInnes 1980). Generally, over 50% of all gosling Barnacle Geese (*Branta leucopsis*) leave their parents by December and <20% remain with their parents until April; however, this distribution varies among years (Black et al. 2007). We observed more families in winter 2003–2004; family breakup on our study area

TABLE 2. Frequencies of social encounters (*n*/hr) of focal Lesser Snow Geese and Ross's Geese, and odds of their success in social encounters in the rice prairies of southwest Louisiana during winters, 2002–2003 and 2003–2004.

	Lesser Snow Geese		Ross's Geese	
Types and success of social encounters	2002–2003	2003–2004	2002–2003	2003–2004
Intraspecific social encounters/hr	0.9	1.0	0.2	0.5
Percentage of intraspecific social encounters won	27.8	45.1	50.0	72.0
Interspecific social encounters/hr	0.3	0.1	0.6	0.5
Percentage of interspecific social encounters won	57.6	97.0	42.4	3.0
Odds of interspecific success[a]	3.53	39.36	0.74	0.01

[a] Odds of interspecific success = odds of winning against other species/odds of winning against own species.

may have occurred earlier for both species in winter 2002–2003 than in winter 2003–2004.

Interspecific Dominance and Mixed Flocks.—Snow Geese were dominant over Ross's Geese, as indicated by their relatively higher odds of winning against Ross's Geese. We did not observe a Ross's Goose win a social encounter against a Snow Goose in a family group. The relatively higher success of Snow Geese in interspecific encounters in 2003–2004 corresponded to a higher frequency of families in that year. Effects of species and family maintenance on outcomes of social encounters probably are confounded; Snow Geese may be more successful in interspecific social encounters because they maintain families. Similarly, family maintenance, rather than species or body size may explain different time-budgets of the two species (Jónsson and Afton 2008). Single-species flocks are known for both species in other locations (Johnson and Raveling 1988, Ryder and Alisauskas 1995, Mowbray et al. 2000), but we only observed one single-species flock of Ross's Geese, in winter 2003–2004 (Jónsson 2005).

Predator vigilance (via "many eyes" and dilution effect) probably is an important benefit of mixed flocking in both species (Kristiansen et al. 2000, Krause and Ruxton 2002, Beauchamp 2003, Randler 2004). Predators may find it increasingly difficult to select prey, when prey choice requires choice of differing types and each prey type has differing cost-benefit relationships for the predator (confusion effect; Sinclair 1985, FitzGibbon 1990, Krause and Ruxton 2002). Snow Geese may have relatively better predator detection capacities because they are taller (cf. Randler 2004) and may have greater visual acuity, given acuity is positively correlated with eye size, which scales positively with body size (Fernandez-Juricic et al. 2004). We often observed Red-tailed Hawks (*Buteo jamaicensis*) fly by the geese, causing them to respond by becoming alert. Bald Eagles (*Haliaeetus leucocephalus*) also attacked goose flocks (Jónsson 2005).

Ross's Geese within mixed flocks evade predators by (1) remaining close to Snow Geese, thus, exposing Snow Geese to avian predators potentially chasing Ross's Geese (cf. Sinclair 1985, FitzGibbon 1990), and (2) remaining well within flock boundaries (JEJ, pers. obs.; R. C. Drewien, pers. comm.). Thus, dominance of Snow Geese seemingly does not drive Ross's Geese towards flock edges; individuals on flock edges often are subordinates (Black et al. 1992).

Mixed flocks probably have been common throughout evolutionary history of these goose species; recent genetic studies show that gene flow is frequent between Snow Geese and Ross's Geese over historical time (Weckstein et al. 2002). New pairs are formed on wintering grounds or during spring migration (Ganter et al. 2005); thus, the two species exchange genetic material via mutual wintering areas (Mowbray et al. 2000). We suggest that along with predation pressure (cf. McWilliams et al. 1994), the historical association of Ross's Geese with Snow Geese, along with the former's associated subordinate social status, has selected against family maintenance in Ross's Geese. However, we observed a small proportion of Ross's Geese in families each winter. Thus, family maintenance probably represents individual choice within a species, rather than a species-fixed evolutionary constraint (Black et al. 2007).

ACKNOWLEDGMENTS

Our study was funded by the Canadian Wildlife Service, Louisiana Department of Wildlife and Fisheries (LDWF), Delta Waterfowl Foundation, Rockefeller Scholarship program, a Research Partnership Proposal (RPP) Grant from Cameron Prairie National Wildlife Refuge (NWR) and the U.S. Fish and Wildlife Service, and by the U.S. Geological Survey-Louisiana Cooperative Fish and Wildlife Research Unit, Graduate School, School of Renewable Natural Resources at Louisiana State University (LSU), and LSU AgCenter. Rockefeller State Wildlife Refuge, Cameron Prairie NWR, and LDWF provided housing and valuable logistical support. We thank C. J. Michie, Brandt Meixell, M. G. Pollock, T. W. Blair, and J. M. Yurek for help with data collection, and D. C. Blouin and M. D. Kaller for advice on statistical analyses. We thank R. N. Helm, Guthrie Perrie, T. J. Hess, J. T. Linscombe, and Daniel Gary for valuable assistance with our project. We acknowledge D. G. Homberger, W. G. Henk, M. J. Chamberlain, S. R. McWilliams, and an anonymous referee for suggestions that improved this paper.

LITERATURE CITED

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, New York, USA.

Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphomet-

rics of midcontinent Lesser Snow Geese. Auk 115:851–862.

Alisauskas, R. T., C. D. Ankney, and E. E. Klaas. 1988. Winter diets and nutrition of midcontinental Lesser Snow Geese. Journal of Wildlife Management 52:403–414.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49:227–267.

Bateman, H. A., T. Joanen, and C. D. Stutzenbaker. 1988. History and status of midcontinent Snow Geese on their Gulf Coast winter range. Pages 495–515 *in* Waterfowl in winter (M. W. Weller, Editor). University of Minnesota Press, Minneapolis, USA.

Beauchamp, G. 2003. Group-size effects on vigilance: a search for mechanisms. Behavioural Processes 63:111–121.

Black, J. M. and M. Owen. 1989a. Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. Animal Behaviour 37:199–209.

Black, J. M. and M. Owen. 1989b. Parent-offspring relationships in wintering Barnacle Geese. Animal Behaviour 37:187–198.

Black, J. M., C. Carbone, and M. Owen. 1992. Foraging dynamics in goose flocks: the cost of living on the edge. Animal Behaviour 44:41–50.

Black, J. M., J. Prop, and K. Larsson. 2007. Wild goose dilemmas. Branta Press, Groningen, The Netherlands.

Boyd, H. 1953. On encounters between wild White-fronted Geese in winter flocks. Behaviour 5:85–129.

Calder III, W. A. 1996. Size, function and life history. Second Edition. Dover Publications, Mineola, New York, USA.

Demment, M. W. and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. American Naturalist 125:641–672.

Fernandez-Juricic, E., J. T. Erichsen, and A. Kacelnik. 2004. Visual perception and social foraging in birds. Trends in Ecology and Evolution 19:25–31.

Fernandez-Juricic, E., G. Beauchamp, and B. Bastain. 2007. Group-size and distance-to-neighbor effects on feeding and vigilance in Brown-headed Cowbirds. Animal Behaviour 73:771–778.

FitzGibbon, C. D. 1990. Mixed species grouping in Thompson and Grant gazelles: the anti-predator benefits. Animal Behaviour 39:1116–1126.

Fox, A. D. and J. Madsen. 1981. The pre-nesting behaviour of the Greenland White-fronted Goose. Wildfowl 32:48–54.

Fronczak, D. 2004. Waterfowl harvest and population survey data. USDI, Fish and Wildlife Service, Division of Migratory Bird Management, Columbia, Missouri, USA.

Ganter, B., W. S. Boyd, V. V. Baranyuk, and F. Cooke. 2005. First pairing in Snow Geese *Anser caerulescens*: at what age and at what time of year does it occur? Ibis 147:57–66.

Gawlik, D. E. 1994. Competition and predation as processes affecting community patterns of geese. Dissertation. Texas A&M University, College Station, USA.

Goudie, R. I. and C. D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482.

Gregoire, P. E. and C. D. Ankney. 1990. Agonistic behavior and dominance relationships among Lesser Snow Geese during winter and spring migration. Auk 107:550–560.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48:215–267.

Johnson, J. C. and D. G. Raveling. 1988. Weak family associations in Cackling Geese during winter: effects of body size and food resources on goose social organization. Pages 71–89 *in* Waterfowl in winter (M. W. Weller, Editor). University of Minnesota Press, Minneapolis, USA.

Jónsson, J. E. 2005. Effects of body size on goose behavior: Lesser Snow Geese and Ross's Geese. Dissertation. Louisiana State University, Baton Rouge, USA.

Jónsson, J. E. and A. D. Afton. 2006. Different time and energy budgets of Lesser Snow Geese in rice prairies and coastal marshes in southwest Louisiana. Waterbirds 29:451–458.

Jónsson, J. E. and A. D. Afton. 2008. Time budgets of Snow Geese and Ross's Geese in mixed flocks: implications of body size, ambient temperature and family associations. Ibis 150:In press.

Jónsson, J. E., A. D. Afton, and R. T. Alisauskas. 2007. Does body size influence nest attendance? A comparison of Ross's Geese (*Chen rossii*) and the larger, sympatric Lesser Snow Geese (*C. caerulescens caerulescens*). Journal of Ornithology 148:549–555.

Kalmbach, E. 2006. Why do goose parents adopt unrelated goslings? A review of hypotheses and empirical evidence, and new research questions. Ibis 148:66–78.

Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of a bird. Condor 72:60–65.

Krause, J. and G. D. Ruxton. 2002. Living in groups. Oxford series in ecology and evolution. Oxford University Press, Oxford, United Kingdom.

Kristiansen, J. N. and N. S. Jarrett. 2002. Inter-specific competition between Greenland White-fronted Geese *Anser albifrons flavirostris* and Canada Geese *Branta canadensis interior* moulting in West Greenland: mechanisms and consequences. Ardea 90:1–13.

Kristiansen, J. N., A. D. Fox, H. Boyd, and D. A. Stroud. 2000. Greenland White-fronted Geese *Anser albifrons flavirostris* benefit from feeding in mixed-species flocks. Ibis 142:139–158.

Loonen, M. J. J. E., L. W. Bruinzeel, J. M. Black,

AND R. DRENT. 1999. The benefit of large broods in Barnacle Geese: a study using natural and experimental manipulations. Journal of Animal Ecology 68:753–768.

MADSEN, J. 1985. Habitat selection of farmland geese in West Jutland, Denmark: an example of a niche shift. Ornis Scandinavica 16:140–144.

MCWILLIAMS, S. R. AND D. G. RAVELING. 1998. Habitat use and foraging behavior of Cackling Canada and Ross's geese during spring: implications for the analysis of ecological determinants of social behavior. Pages 167–178 *in* Biology and management of Canada Geese (M. D. Samuel, Editor) Proceedings of the International Canada Goose symposium, Milwaukee, Wisconsin, USA.

MCWILLIAMS, S. R., J. P. DUNN, AND D. G. RAVELING. 1994. Predator-prey interactions between eagles and Cackling Canada and Ross's geese during winter in California. Wilson Bulletin 106:272–288.

MOWBRAY, T. B., F. COOKE, AND B. GANTER. 2000. Snow Goose (*Chen caerulescens*). The birds of North America. Number 514.

PREVETT, J. P. AND C. D. MACINNES. 1980. Family and other social groups in Snow Geese. Wildlife Monographs 71.

RANDLER, C. 2004. Coot benefit from feeding in close proximity to geese. Waterbirds 27:240–244.

RAVELING, D. G. 1970. Dominance relationships of agonistic Canada Geese in winter. Behaviour 37: 291–319.

RYDER, J. P. AND R. T. ALISAUSKAS. 1995. Ross's Goose (*Chen rossii*). The birds of North America. Number 162.

SAS INSTITUTE. 1999. SAS/SYSTAT users guide. Version 8. SAS Institute, Cary, North Carolina, USA.

SHELLEY, E. L., M. Y. U. TANAKA, A. R. RATNATHICAM, AND D. T. BLUMSTEIN. 2004. Can Lanchester's laws help explain interspecific dominance in birds? Condor 106:395–400.

SINCLAIR, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? Journal of Animal Ecology 54:899–918.

STAHL, J., P. H. TOLSMA, M. J. J. E. LOONEN, AND R. H. DRENT. 2001. Subordinates explore but dominants profit: resource competition in high Arctic Barnacle Goose flocks. Animal Behaviour 61: 257–264.

WECKSTEIN, J. D., A. D. AFTON, R. M. ZINK, AND R. T. ALISAUSKAS. 2002. Hybridization and population subdivision within and between Ross's Geese and Lesser Snow Geese: a molecular perspective. Condor 104:432–436.

The Wilson Journal of Ornithology 120(4):732–742, 2008

NESTING ECOLOGY OF COMMON GOLDENEYES AND HOODED MERGANSERS IN A BOREAL RIVER SYSTEM

HÉLÈNE SÉNÉCHAL,[1] GILLES GAUTHIER,[1,3] AND JEAN-PIERRE L. SAVARD[2]

ABSTRACT.—Common Goldeneyes (*Bucephala clangula*) and Hooded Mergansers (*Lophodytes cucullatus*) are common cavity-nesting ducks but the importance of fast-flowing rivers as suitable nesting habitat may have been overlooked. We monitored the use of >90 nest boxes installed along a boreal forest river over a 5-year period. A high nest box occupancy rate was reached in the second year (40%) and was maintained thereafter (48 to 55%). On average, 35 nest boxes were occupied by goldeneyes and 11 by mergansers each year. Laying date was similar between the two species but merganser nests hatched slightly later. Both species had similar clutch sizes but merganser nests contained more eggs than goldeneye nests when heterospecific parasitic eggs were included. On average, 16% of goldeneye nests were parasitized by mergansers, and 49% of merganser nests were parasitized by goldeneyes. Density of suitable natural cavities in the area was relatively low suggesting the high occupancy rate of nest boxes may be a response to lack of suitable cavities. Nest box use was positively related to the total surface area of ponds in the vicinity and negatively to distance to the river. Use of nest sites along fast-flowing rivers appears to be an opportunistic strategy and may be dependant on the presence of nearby ponds and lakes. *Received 1 October 2007. Accepted 23 February 2008.*

Selection of a suitable nest site is of critical importance for breeding birds because it can influence their reproductive success. A good nest site must be safe from predators, and provide shelter from bad weather and extreme environmental conditions. Ideally, it should also be in an area with abundant food resources. A strategy used by many bird species is to nest in tree cavities. This strategy benefits these species by providing a favorable microclimate for eggs and young, and decreases nest predation risks (Nilsson 1986).

Common Goldeneye (*Bucephala clangula*) and Hooded Merganser (*Lophodytes cucullatus*) are secondary cavity-nesting ducks that breed in the boreal forest (Dugger et al. 1994, Eadie et al. 1995). These species are relatively large and require large cavities, which represent only a small proportion of all cavities available in the boreal forest (Gauthier and Smith 1987). Intra- and interspecific competition for these large cavities is therefore severe (Erskine 1990, Semel and Sherman 2001). Selection of a suitable nest site may be especially critical in regions of intensive forest management because forestry practices can reduce the availability of suitable cavities. Many studies have shown that addition of nest boxes results in increases in breeding populations of secondary cavity-nesters (Savard 1988, Newton 1994, Pöysä and Pöysä 2002) suggesting that nest site availability was limiting these populations at least locally.

Common Goldeneyes and Hooded Mergansers commonly breed on ponds and lakes of the boreal forest. Fast-flowing rivers, although abundant throughout the boreal forest, are generally not considered an important breeding habitat for these species (Eadie et al. 1995). Nest site selection of Common Goldeneyes has been previously studied in lake systems (Lumsden et al. 1980, 1986), but the nesting biology of these species in river systems is little known. The overall objective of this study was to evaluate the potential of rivers as nesting habitat for Common Goldeneyes and Hooded Mergansers in the boreal forest. We studied the nesting ecology of both species using nest boxes in a fast-flowing river system in the Quebec boreal forest. We also assessed the potential for nest site competition between both species and investigated whether occupancy of nest boxes along the river could be associated with a scarcity of natural cavities in the area. Finally, we identified river characteristics and components of the riparian habitat influencing nest site selection and nesting success of these species in this habitat.

[1] Département de Biologie and Centre d'études Nordiques, Pavillon Vachon, 1045 Avenue de la Médecine, Université Laval, Québec, PQ G1V 0A6, Canada.

[2] Science and Technology, Environment Canada, 1141, Route de l'Église, C.P. 10100, 9e étage, Québec, PQ, G1V 4H5, Canada.

[3] Corresponding author; e-mail: gilles.gauthier@bio.ulaval.ca

METHODS

Study Area.—This study was conducted in the Ste. Marguerite River Valley (48° 23′ N, 70° 12′ W), 200 km northeast of Quebec City, Canada. This is a meandering but fast flowing river typical of the boreal forest in Quebec (mean annual discharge = 58 m^3/sec). The river flows for ~100 km in a 0.5–1.0 km wide valley, often bordered by steep mountain slopes rising to 350 m above the valley bottom. About 53 ponds (including oxbows) occur in the valley of the studied section and can be used by breeding adults or broods after hatch. The Ste. Marguerite River is a prime Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) fishery managed by a private fishing association.

Mature stands of balsam fir (*Abies balsamea*) and yellow birch (*Betula alleghaniensis*) dominate the forest of the valley. The forest in the upper half of the study area has remained almost untouched for at least 100 years and large yellow birch trees are abundant. However, clear-cutting occurred in the early 1980's on about 6% of the catchment area, mainly in the lower half of the valley; this area still has some 80-year-old trees.

Experimental Design.—Ninety-two nest boxes were erected in fall 1997 along a 50-km stretch of the river, encompassing a diversity of river habitats (rapids, fast current, slow current, meanders, etc.); 10 additional boxes were installed in fall 2000. The number of boxes varied annually from 82 to 93 because some nest boxes were damaged by falling trees or disappeared. Their distribution along the river followed fishing access paths in most cases but boxes were isolated from fishing pools to minimize human disturbance. Boxes were separated by at least 30 m and nailed to trees close to the water edge (range = 0 to 29 m) with the entrance hole facing the river, between 2 and 5 m above the ground. Boxes were made of plywood (inside dimensions: 23 × 26 × 58 cm; entrance: 10 × 12 cm; depth below the entrance: 45 cm) and a 10-cm layer of wood shavings was added as nest material. We removed branches in front of the boxes to ensure visibility from the river and ease of entry for waterfowl. Boxes were cleaned at the end of each breeding season (abandoned eggs removed) and wood shavings were changed.

Nest Box Monitoring and Measurement of Nesting Parameters.—Nest boxes were monitored from early May to early July weekly in 2001, three times in 2000 and 2002, and twice in 1998 and 1999. We recorded the number of eggs of each species and boxes containing eggs of more than one species were identified as interspecific nest parasitism. The species that first started the nest or, if unknown, the incubating species was considered the host. Eggs were numbered with a permanent marker, and measured (length and width, ±0.1 mm) with a caliper and weighed (±1 g) with a spring scale. These measurements were used to calculate the Maximum Euclidian Distance (MED), a criterion used to identify intraspecific nest parasitism (Eadie 1989, Pöysä et al. 2001). Nests were classified as parasitized by conspecifics when at least one of the following criteria was met: (1) the MED among the eggs was >2.5, (2) clutch size was >12 eggs, (3) more than one egg was laid per day, and (4) eggs were laid two or more days after the start of incubation. More than one of these criteria was met in most nests where parasitism was detected. These criteria should yield a minimum estimate of nest parasitism (Andersson and Åhlund 2001).

We calculated the date on which the first egg of the clutch was laid (i.e., laying date) for nests discovered during laying by backdating using the number of eggs of the host species at the time of discovery (maximum of 12 eggs; additional eggs were considered parasitic) and assuming a mean laying rate of one egg every 1.4 days. The laying date for nests discovered during incubation was backdated from the hatching date assuming an incubation period of 30 days. We calculated hatching date when it was unknown (for some nests in 2000 and 2002), using the relationship between incubation stage and egg density (Sénéchal 2003). We estimated the age of embryos (Caldwell and Snart 1974) for deserted nests with unknown laying dates and backdated the laying date. Clutch size was defined as the highest number of eggs recorded in an incubated nest.

Nesting success was the proportion of successful nests (i.e., those in which at least one egg hatched). Deserted nests were those aban-

doned during laying or incubation with no signs of predation and were included in the calculation of nesting success. Hatching success, defined as the proportion of eggs that hatched within a clutch, was calculated for successful nests.

Availability of Natural Cavities.—We estimated the availability of living trees and snags sufficiently large to support cavities and of cavities along the river using line transect sampling (Buckland et al. 1993). We positioned 17, 300-m transects every 3 km at right angle to the river axis. We recorded the position and perpendicular distance from the transect of all trees and snags ≥30 cm in diameter at breast height (DBH) encountered. We ascertained species, height, DBH, and presence of cavities with entrance diameter ≥8 cm (visual estimate from the ground) for these trees. We recorded the cavity type (hollow top of standing trees, woodpecker hole, broken tree limbs, or crack on the side of a tree), its height above ground, an index of its accessibility from the air (under the canopy, in the canopy, over the canopy, or open forest), and the approximate size of the entrance hole. Any signs of waterfowl use (e.g., presence of down at the entrance) were noted. Cavities with entrances ≥8 cm, ≥1.8 m above ground, and easily accessible (i.e., above the forest canopy or in an open stand) were considered suitable (Bergeron et al. 1997). Sampling was conducted in late May-early June and at the end of July 2001.

Nest Site Characterization.—We sampled the habitat surrounding each nest box in late July-early August 2001. We measured river depth at the deepest point with a graduated rod, river width with a measuring tape (at times estimated from the shore), and surface water velocity at the deepest point using a portable current meter (Marsh McBirney, model 201M; Frederick, MD, USA). We combined velocity measurements and the general aspect of the river to create a new variable that categorized river sections as rapids (≥60 cm/sec with riffles at the surface), fast-flowing (≥60 cm/sec, water surface still) or slow-flowing (<60 cm/sec).

We sampled 12 terrestrial habitat variables at each nest box. These variables included: distance to water edge, to nearest lake or pond, to nearest used nest box, and to nearest tree ≥10 cm in diameter; entrance height above the river and above the ground; compass direction faced by the entrance (categorized as North, East, South, or West); and canopy height. Distances to nearest pond or nest box were obtained from a digital map (scale: 1:20,000) whereas other distance variables were measured in the field. We also sampled density of trees with a DBH of ≥20 cm in a semi-circle centered in front of the nest box (11.3-m radius) and evaluated shrub height. Stems ≥4 m in height were defined as trees and those <4 m as shrubs. We also counted the number of lakes and ponds in the vicinity on the digital map, i.e., those included in a 2 × 6 km ellipse (long axis parallel to the river) centered at the nest box, and calculated the total surface area of these water bodies.

Data Analysis.—Statistical analyses were completed with software SAS 8.0 (SAS Institute 1999). Interactions in analyses with more than one factor were examined and removed from the model when non significant ($P > 0.05$).

We examined the effects of species and year on laying date, hatching date, and clutch size with two-way ANOVAs. Dates were rank-transformed and we used the ART procedure to test the interaction as recommended by Salter and Fawcett (1993). We examined the effects of year, species, and parasitic egg laying on nesting success using a log-linear analysis. We analyzed the effect of egg status (host species in a parasitized nest, heterospecific parasite in a parasitized nest, or in a nest non-parasitized by a heterospecific parasite), year, and species on hatching success using a three-way ANOVA on rank-transformed data. We examined the effects of species and year on the rate of parasitism using logistic regressions, and on the number of heterospecific parasitic eggs using two-way ANOVAs. We compared the laying date of parasitized and non-parasitized nests of each species using ANOVA.

We estimated densities of living trees (≥30 cm DBH), snags, and cavities with DISTANCE 3.5 (Buckland et al. 1993, Research Unit for Wildlife Assessment 1999). We compared DBH and height between snags and living trees using Mann-Whitney tests, and the proportion of trees with cavities using χ^2. We examined if snag and living tree densities,

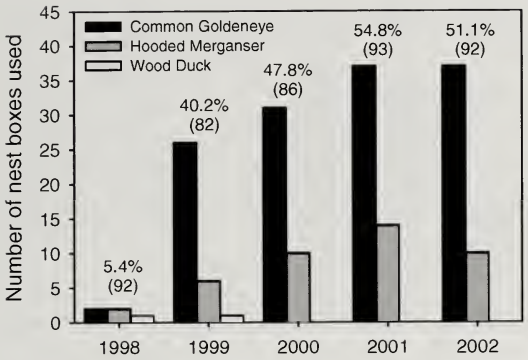


FIG. 1. Nest boxes used by waterfowl in the Ste. Marguerite River Valley, Québec, Canada, 1998–2002. Percentages are based on the total number of boxes used by waterfowl and numbers in parentheses are the annual number of boxes available. Data for 1998 and 1999 are from Nadia Aubin-Horth (pers. comm.).

cavity abundance (because of the small number of suitable cavities found), and tree characteristics (DBH, height) were related to distance to the river (in 50-m classes) with linear regression.

We generated three independent data sets to analyze characteristics of nest sites used by each species from 1999 to 2002. Boxes were classified whether they were used: (1) at least once versus not used, (2) at least twice versus not used, and (3) at least three times versus not used. Separate analyses with each data set generally yielded similar results (Sénéchal 2003), and we present only the results based on boxes used at least twice because this avoided using data from boxes rarely used (i.e., only once) while retaining sufficient sample size. The effect of the 13 quantitative habitat variables on nest site use was first analyzed using a stepwise discriminant analysis, followed by a logistic regression including variables retained by the first analysis ($P <$ 0.15) and qualitative variables. We used the same procedure to test the relationship between nesting success and habitat characteristics for goldeneyes (sample sizes were too small for mergansers). We combined data from 2000 to 2002 and, for nests used more than once, we assigned success or failure based on the occurrence that was most frequent, excluding those with the same number of successes and failures.

RESULTS

Nest Box Use and Nesting Parameters.— The number of nest boxes used by waterfowl was low the first year but increased in the second year (Fig. 1). Occupancy rate stabilized at 51–55% by the fourth year of the program. Goldeneye use of nest boxes outnumbered mergansers three to four times in all years but the first.

Both species started their clutches at about the same time from 2000 to 2002 ($F_{1,109} = 2.0$, $P = 0.17$) with no differences between years ($F_{2,109} = 1.8$, $P = 0.18$). Overall, mean (±SE) laying date was 4 May ± 0.9 days (range = 14 Apr–24 May, $n = 81$) for goldeneyes and 7 May ± 1.9 days (21 Apr–5 Jun, $n = 34$) for mergansers. Goldeneye nests hatched slightly earlier than mergansers ($F_{1,90} = 5.8$, $P = 0.02$). Overall, the mean hatching date was 15 Jun ± 0.9 days (31 May–2 Jul, $n = 68$) for goldeneyes and 20 Jun ± 1.9 (31 May–13 Jul, $n = 28$) for mergansers.

Mean (±SE) clutch size in incubated goldeneye nests (9.8 ± 0.4 eggs, $n = 78$) was similar to that of mergansers (9.2 ± 0.5, $n = 33$; $F_{1,107} = 0.8$, $P = 0.36$) when eggs resulting from interspecific parasitism were excluded and did not vary among years ($F_{2,107} = 0.2$, $P = 0.83$; Table 1). The total number of eggs (i.e., including parasitic eggs) was higher for

TABLE 1. Mean [± SE] clutch size (sample size) of the host species only and total clutch size (including interspecific parasitic eggs) in incubated nests of Common Goldeneyes and Hooded Mergansers, Ste. Marguerite River, Québec, Canada, 2000–2002.

	Host species clutch only			Total clutch		
Species	2000	2001	2002	2000	2001	2002
Common Goldeneye	9.2 ± 0.5 (23)	9.7 ± 0.5 (31)	10.3 ± 0.8 (24)	9.8 ± 0.6 (23)	10.0 ± 0.6 (31)	11.0 ± 0.9 (24)
Hooded Merganser	10.0 ± 1.2 (10)	8.7 ± 0.5 (13)	8.9 ± 0.7 (10)	12.7 ± 0.9 (10)	11.5 ± 1.0 (13)	10.4 ± 1.2 (10)

TABLE 2. Percent nesting success (sample size) of Common Goldeneyes and Hooded Mergansers in nest boxes, Ste. Marguerite River, Québec, Canada, 2000–2002.

Host species	Parasitized nests[a]			Non-parasitized nests			All nests		
	2000	2001	2002	2000	2001	2002	2000	2001	2002
Common Goldeneye	86 (7)	67 (15)	85 (13)	79 (24)	64 (22)	50 (24)	81 (31)	65 (37)	62 (37)
Hooded Merganser	100 (8)	88 (8)	75 (4)	100 (2)	67 (6)	67 (6)	100 (10)	79 (14)	70 (10)

[a] Intraspecific and interspecific nest parasitism.

merganser nests (11.6 ± 0.6) than for goldeneye nests (10.2 ± 0.4; $F_{1,107} = 3.7$, $P = 0.06$).

Nesting success of both species decreased between 2000 and 2002 ($\chi^2_2 = 16.1$, $P < 0.01$), and was lower for goldeneyes than for mergansers ($\chi^2_1 = 3.3$, $P = 0.07$; Table 2). Non-parasitized nests were less successful than those parasitized (64 vs. 82%, $\chi^2_1 = 8.8$, $P < 0.01$). Desertion was the main cause of nesting failures of goldeneyes (54%, $n = 28$). Other causes included desertion due to marking (18%), death of incubating females (7%), clutch predation (7%), other human disturbance (7%), and unknown (4%). The main cause of nest failure for mergansers was desertion due to human disturbance other than marking (33%, $n = 6$). Other causes included clutch predation (17%) and unknown (50%).

Overall, heterospecific parasitic eggs did not fail more often than eggs from host species or eggs in non-parasitized nests ($F_{2,107} = 0.2$, $P = 0.80$; Table 3). Goldeneyes and mergansers had similar hatching success (90 vs. 88% overall, $F_{1,107} = 0.4$, $P = 0.56$) and there were no differences between years ($F_{2,107} = 2.3$, $P = 0.11$).

Pattern of Nest Parasitism.—Interspecific nest parasitism started in the second year (1999) of the nest box program and appeared to increase with the proportion of nest boxes used (Fig. 2; year effect: $\chi^2_3 = 5.6$, $P = 0.13$). A much greater proportion of merganser nests were parasitized by goldeneyes than the reverse ($\chi^2_1 = 8.6$, $P < 0.01$). Parasitized merganser nests also contained on average more goldeneye eggs (4.7 ± 0.6 eggs, $n = 17$) than the reverse (2.8 ± 0.3, $n = 16$; $F_{1,29} = 7.2$, $P = 0.01$).

Parasitism by conspecifics was also common in both species (species effect: $\chi^2_1 = 0.5$, $P = 0.49$), ranging from 9 to 32% of goldeneye and 7 to 30% of merganser nests during 2000–2002 (year effect: $\chi^2_2 = 3.2$, $P = 0.20$). Among the total number of nests initiated by each species (i.e., nests where each species laid at least 1 egg), mergansers tended to lay more often as a parasite (intra- and interspecific egg laying combined) than goldeneyes ($\chi^2_1 = 3.2$, $P = 0.07$; Fig. 3). On average, 25 ± 5% (range = 18–35%) of all nests containing goldeneye eggs were associated with parasitic events by this species compared to 39 ± 8% (22–50%) for mergansers. Nests parasitized by goldeneyes (intra- and interspecifically) were initiated earlier (30 Apr ± 1.3 days, $n = 31$) than non-parasitized nests (6 May ± 1.1, $n = 50$; $F_{1,77} = 9.1$, $P < 0.01$); this was not the case for mergansers ($F_{1,29} = 2.2$, $P = 0.15$).

TABLE 3. Mean [± SE] percent hatching success (sample size) of Common Goldeneyes and Hooded Mergansers in successful nest boxes, Ste. Marguerite River, Québec, Canada, 2000–2002.

Species	Parasitized nests[a]						Non-parasitized nests		
	Host species eggs			Heterospecific parasitic eggs					
	2000	2001	2002	2000	2001	2002	2000	2001	2002
Common Goldeneye	84 ± 16 (5)	83 ± 4 (2)	79 ± 8 (7)	100 (6)	76 ± 10 (7)	67 ± 17 (2)	97 ± 2 (17)	91 ± 2 (22)	96 ± 3 (15)
Hooded Merganser	85 ± 9 (6)	85 ± 9 (7)	100 (2)	93 ± 7 (5)	83 ± 17 (2)	87 ± 10 (7)	90 ± 5 (4)	89 ± 8 (4)	90 ± 5 (5)

[a] Interspecific nest parasitism.

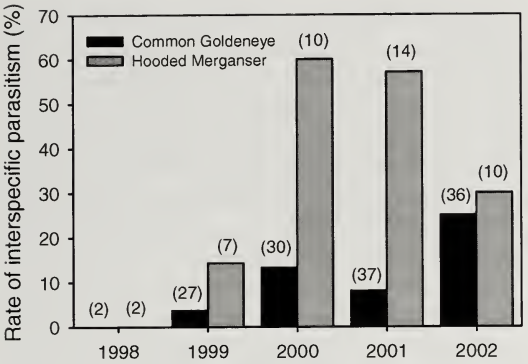


FIG. 2. Common Goldeneye and Hooded Merganser nests parasitized by a heterospecific, Ste. Marguerite River, Québec, Canada, 1998–2002. Numbers in parentheses are number of nests.

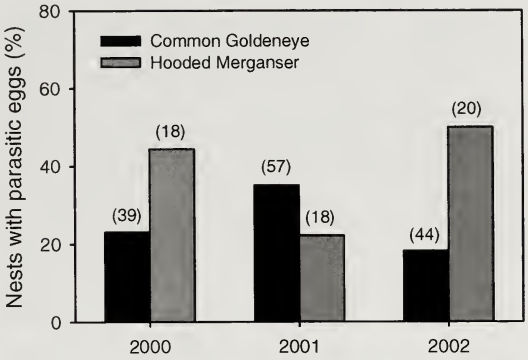


FIG. 3. Nests that contained eggs that were laid parasitically (either intra- or interspecifically) by Common Goldeneyes among all nests initiated by this species (i.e., nests where goldeneyes laid at least 1 egg), and vice-versa for Hooded Mergansers, Ste. Marguerite River, Québec, Canada, 2000–2002. Numbers in parentheses are number of nests.

Availability and Suitability of Natural Cavities.—Of 688 trees (≥ 30 cm DBH) recorded along transects, 17% were snags and 83% were alive. Large snag density was estimated at 6.5 ± 0.8 snags/ha, almost six times lower than large living trees (36.6 ± 2.0 trees/ha). Snags were slightly larger (mean DBH: 42.4 ± 0.8 cm, n = 114) than living trees (40.4 ± 0.4 cm, n = 574; U = 5.9, P = 0.02), but shorter (7.8 ± 0.7, n = 45 vs. 18.1 ± 0.3 m, n = 204, respectively; U = 82.6, $P < 0.01$).

Suitable cavities were present in 6% of the snags (n = 114; 1 with 2 cavities) but were rarely found in living trees (1%, n = 574; χ^2_1 = 32.3, $P < 0.01$). We found 16 suitable cavities during sampling for an estimated density of 0.92 ± 0.31 cavity/ha, but none had signs of waterfowl use. Thirty-seven cavities sufficiently large for ducks were found (1.71 ± 0.37 cavities/ha) when the accessibility criterion was not considered. Pileated Woodpecker (*Dryocopus pileatus*) holes were the most abundant cavity type (50%), followed by chimney cavities (38%) and natural cracks (12%). Most suitable cavities were in snags (69%) at a mean height of 6.2 ± 1.0 m (n = 11).

The dominant species of large trees were yellow birch (57%), balsam fir (19%), eastern white cedar (*Thuja occidentalis*; 7%), and white spruce (*Picea glauca*; 6%). Black ash (*Fraxinus nigra*), eastern white pine (*Pinus strobus*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and white elm (*Ulmus americana* L.) each accounted for ≤3% of the large trees. The 16 suitable cavities were mainly in yellow birch (81%); the rest were equally distributed among elm, ash, and fir (6% each).

Yellow birch was the only tree species for which density increased with distance to the river up to 300 m (β = 3.73 ± 0.47 trees/ha/50 m, r^2 = 0.94, $P < 0.01$, n = 6). Density of large snags decreased away from the river (β = −0.87 ± 0.37 snags/ha/50 m, r^2 = 0.58, P = 0.01). There was no relationship between the abundance of suitable cavities and distance to the river (r^2 = 0.17, P = 0.41), nor between tree height or DBH and distance to the river ($P > 0.12$).

Nest Site Characteristics.—Only 19 of all nest boxes available were not used. Boxes in the upper half of the river were generally used more often than those in the lower half. Few habitat variables explained nest box use by ducks. Boxes used by goldeneyes had a greater total surface area of ponds in the vicinity (40.7 ± 6.1 ha) than those not used (8.3 ± 4.0 ha) and goldeneyes used boxes predominantly oriented toward the south (Table 4). Boxes not used by this species were usually farther from water than those used (9.4 ± 1.2 vs. 6.2 ± 0.7 m, respectively). Used boxes were farther from trees ≥10 cm (2.4 ± 0.3 m) than those not used (1.5 ± 0.2 m). Goldeneye nesting success was affected mainly by the total surface area of ponds in the vicinity (χ^2_1 =

TABLE 4. Characteristics explaining use by Common Goldeneyes and Hooded Mergansers for nest boxes used at least 2 years, Ste. Marguerite River, Québec, Canada, 1998–2002. '+' indicates a positive effect and '−' indicates a negative effect. Numbers in parentheses are the number of used vs. unused boxes.

Species	Variables[a]	Effect	*P*
Common Goldeneye	SURFPOND	+	0.003
	ORIEN	S+	0.047
	DISWAT	−	0.004
	DISTREE	+	0.032
		(37 vs. 27)	
Hooded Merganser	CANOP	+	<0.001
	DISTREE	+	0.006
		(8 vs. 55)	

[a] SURFPOND: total surface area of ponds, ORIEN: compass direction faced by the nest box entrance (S = South), DISWAT: distance to the water edge, DISTREE: distance to the nearest tree ≥10-cm diameter, and CANOP: canopy height.

13.2, $P < 0.01$); failed nests were surrounded by a larger surface of ponds than those that were successful (61.6 ± 15.0 ha, $n = 14$ vs. 35.5 ± 7.9, $n = 36$, respectively).

Boxes used by mergansers were also farther from the nearest tree ≥10 cm in diameter than those not used (3.3 ± 0.7 vs. 2.0 ± 0.2 m), and tree canopy around used boxes (21.8 ± 2.4) was higher than around boxes not used (14.5 ± 0.7, Table 4).

DISCUSSION

Nesting Biology.—Common Goldeneye and Hooded Merganser nesting biology in river habitat appears similar to that in the more usual lacustrine habitats of northeastern North America. Nest initiation dates (16 Apr–27 May) reported for goldeneyes in Ontario (Mallory et al. 1994, Eadie et al. 1995) are similar to those in our study. Mean Clutch sizes reported in Ontario (7.4–9.4 eggs), New Brunswick (9.0 eggs), and Minnesota (10.2 eggs) (Eadie et al. 1995) are also similar. Nesting success in our study was higher than reported by Bouvier (1974) in southern Quebec (57%) but lower than observed in Maine (87%) (Allen et al. 1990). Clutch size of Hooded Mergansers usually ranges from nine to 13 eggs and nesting success ranges from 66 to 82% (Dugger et al. 1994, Mallory et al. 2002). This suggests that nesting in habitats adjacent to fast-flowing rivers does not impose severe constraints on nesting phenology or success for these species.

The similarity in the observed breeding phenology of Common Goldeneyes and Hooded Mergansers is not surprising given the similarities in life history traits of the two species (Dugger et al. 1994, Eadie et al. 1995). The few merganser nests initiated after 25 May were possibly renesting attempts or nests of first-time breeders that nest later than older, experienced females (Dow and Fredga 1984).

Desertion was a major cause of nesting failure for goldeneyes. This may be due to a high proportion of first-time breeders in the area, as inexperienced birds are more prone to desertion (Eriksson and Andersson 1982, Gauthier 1989). A high proportion of first-time breeders may result from a recent increase in the breeding population possibly due to installation of nest boxes. Human disturbance may also be a cause of nest desertion of goldeneyes. This species shows relatively weak nest attentiveness and defense relative to Hooded Mergansers, flushing more readily when disturbed (Mallory et al. 1993a, 1998). Greater sensitivity to disturbance may contribute to the high rate of nest abandonment of goldeneyes. It is also possible that more frequent visits to nest boxes in 2001, and more capture and handling of females, contributed to high nest desertion that year.

Nest parasitism often has a negative impact on nesting success of waterfowl due to disturbance by parasitic females (Semel et al. 1988, 1990). This was not the case in our study, as parasitized nests generally had greater nesting success than non-parasitized nests (also reported by Eadie 1989). Large clutches resulting from nest parasitism at times also have reduced hatching success (Mallory et al. 2002), but normal hatching success has also been reported (Eriksson 1979, Eriksson and Andersson 1982, McNicol et al. 1997). Large clutches (>20 eggs) were rare in our study, which may explain why parasitism had little effect on hatching success.

Nest Parasitism and Nest Site Competition.—Intra- and interspecific nest parasitism were both common in our study. The frequency of conspecific egg laying is likely a minimum value because Andersson and Åhlund (2001) showed with biochemical techniques that it is underestimated with traditional methods. Our results support the suggestions of Eadie (1989), Semel et al. (1988), and Haramis

and Thompson (1985) that high breeding densities of cavity-nesting waterfowl and relative scarcity of suitable nest sites may contribute to nest parasitism. Almost half of our nest boxes were unused, apparently suggesting that nest sites were not limiting. However, this assumes that all nest boxes and sites selected for their placement were of equal quality, which is unlikely to be true. We found evidence that goldeneyes preferred some boxes over others. Moreover, boxes were distributed over 50 km of river that may vary greatly in quality for ducks. For example, boxes in the lower half of the river received relatively little use. Thus, even though only 55% of the boxes were used, there could be competition for high quality nest sites.

Merganser nests were more likely to be parasitized by goldeneyes and received a larger number of parasitic eggs than goldeneye nests, as reported in other studies (Bouvier 1974, Mallory et al. 1993a). The greater proportion of parasitized merganser nests may be related to the smaller size of the merganser population rather than a lower propensity for parasitic egg-laying. Mergansers tended to lay more often as a parasite than goldeneyes (also reported by Mallory et al. 1993a) when we compared the number of nests where one species laid parasitically in relation to the number of nests initiated by that species. Intraspecific nest parasitism in cavity-nesting ducks may be an adaptive strategy (Semel et al. 1988, Pöysä 1999, Andersson 2001, Åhlund 2005), but it can also be the outcome of two individuals inadvertently choosing the same nest site to lay their eggs (Erskine 1990). Semel and Sherman (2001) supported this hypothesis for Wood Ducks (*Aix sponsa*) and interspecific nest parasitism is perhaps more likely to result from such nest site competition. Hooded Mergansers are probably dominated in competitive interactions by the larger, more aggressive goldeneye. Thus, they may be more easily evicted from a nest box, giving the impression that mergansers "parasitize" more often than goldeneyes.

Availability and Suitability of Natural Cavities.—No breeding pair surveys were conducted in the area before nest boxes were installed and we do not know with certainty if high use of boxes by goldeneyes and mergansers reflects a real increase of their local populations, as reported for other populations (Fredga and Dow 1984, Savard 1988, Pöysä and Pöysä 2002). One explanation for the increase in nest box use may be that local females moved from nearby natural cavities to the more conspicuous nest boxes near the river (Gauthier and Smith 1987). Our sampling showed that density of suitable cavities was low in our study area considering the high density of large snags and living trees present. Our density estimate for natural cavities may also be a maximum value as we were not able to inspect the interior of cavities. Similar cavity densities have been reported elsewhere (Sénéchal 2003), but the density was lower than expected for a mature forest (Prince 1968, Gilmer et al. 1978). None of the cavities found appeared to be used by waterfowl. Suitable cavities may have been beyond our 300-m transects, but steep slopes or cliffs were often encountered beyond this distance, which would reduce their attractiveness because of predation risks associated with long and difficult overland travel by broods.

Common Goldeneyes appear flexible in the type of cavity used. Carter (1958) mentioned they use mainly lateral openings in New Brunswick, whereas Prince (1968) identified chimney cavities as the main type used. Maisonneuve et al. (2002) reported that half of Hooded Merganser and Common Goldeneye nests found in Québec boreal forest were in old Pileated Woodpecker cavities. Abandoned Pileated Woodpecker holes in our study were the main source of suitable cavities and this woodpecker may be a key species for cavity-nesting ducks (Bonar 2000).

Nest Box Use and Habitat Characteristics.—The preference of goldeneyes for nest boxes in areas with a high surface area of ponds suggests that many pair territories were on ponds. Mallory et al. (1993b) reported goldeneyes preferred nest boxes in wetlands without fish isolated from other water bodies in acid-stressed areas of Ontario. Many lakes and ponds in our study area supported fish and were little acid-stressed, but may provide more invertebrate food than the river where Atlantic salmon were present. An abundance of ponds in the vicinity may also provide many potential brood-rearing sites, as ponds are important brood habitats for females nesting along the river (Sénéchal 2003). Golden-

eyes preferred nest boxes closest to water, presumably because proximity to water minimizes overland travel for broods after hatch (Morse et al. 1969, Pöysä et al. 1999) and decreases predation risks. Nest boxes near water are also more conspicuous than those further in the forest and are more easily found by ducks. The preference for nest boxes far from large trees is another indication that goldeneyes prefer nesting in open habitats. Mergansers also selected nest sites in open habitats with a high canopy. The preference of goldeneyes for boxes with a southward orientation may be related to a more favorable micro-climate (i.e., away from prevailing westerly wind and toward the sun). No characteristics of the river influenced nest box use by either species, but this may not be surprising if pair territories were mostly away from the river. Presence of a suitable cavity (nest box) along the river may be the main stimulus for nesting in this habitat.

Few characteristics of the habitat surrounding nest sites affected goldeneye nesting success. Surprisingly, goldeneye nests with a high surface area of ponds in their vicinity were less successful. Pond area positively influenced nest site use, and the attractiveness of nest sites in these areas may have increased disturbance from prospecting females (Eadie and Gauthier 1985) and may have decreased nesting success. Mallory et al. (1993b) reported that lake isolation was an important factor in nest site selection by goldeneyes in Ontario and suggested that high bird density may lead to interference in this highly territorial species (Savard 1984). Eadie (1989) found no differences in habitat characteristics between successful and failed Barrow's (*Bucephala islandica*) and Common goldeneye nests in British Columbia.

ACKNOWLEDGMENTS

We acknowledge the Fondation de la faune du Québec, Fonds Québécois de Recherche sur la Nature et les Technologies, Natural Sciences and Engineering Research Council of Canada, Canadian Wildlife Service, Ducks Unlimited, and the Centre Interuniversitaire de Recherche sur le Saumon Atlantique for financial support. We also thank Nadia Aubin-Horth, Dominic Savard, Gérald Picard, Grégory Bourguelat, Jérôme Léger, M.-C. Cadieux, Antoine Morrissette, J.-F. Savard, Karine Plante, Catherine Bonenfant, and Félix Ledoux for help in the field, and Jean Huot and Cyrille Barrette for comments on the manuscript.

LITERATURE CITED

Åhlund, M. 2005. Behavioural tactics at nest visits differ between parasites and hosts in a brood-parasitic duck. Animal Behaviour 70:433–440.

Allen, R. B., P. O. Corr, and J. A. Dorso. 1990. Nesting success and efficiency of waterfowl using nest boxes in central Maine: a management perspective. Pages 291–296 *in* Proceedings of the 1988 North American Wood Duck Symposium (L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, Editors). St. Louis, Missouri, USA.

Andersson, M. 2001. Relatedness and the evolution of conspecific brood parasitism. American Naturalist 158:599–614.

Andersson, M. and M. Åhlund. 2001. Protein fingerprinting: a new technique reveals extensive conspecific brood parasitism. Ecology 82:1433–1442.

Bergeron, D., M. Darveau, A. Desrochers, and J.-P. L. Savard. 1997. Impact de l'abondance des chicots sur les communautés aviaires et la sauvagine des forêts conifériennes et feuillues du Québec méridional. Technical Report Series Number 271F. Canadian Wildlife Service, Quebec City, Quebec, Canada.

Bonar, R. L. 2000. Availability of Pileated Woodpecker cavities and use by other species. Journal of Wildlife Management 64:52–59.

Bouvier, J. M. 1974. Breeding biology of the Hooded Merganser in southwestern Quebec, including interactions with Common Goldeneyes and Wood Ducks. Canadian Field-Naturalist 88:323–330.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London, United Kingdom.

Caldwell, P. J. and A. E. Snart. 1974. A photographic index for aging Mallard embryos. Journal of Wildlife Management 38:298–301.

Carter, B. C. 1958. The American Goldeneye in central New Brunswick. Wildlife Management Bulletin 2. Number 9. Canadian Wildlife Service, Ottawa, Ontario, Canada.

Dow, H. and S. Fredga. 1984. Factors affecting reproductive output of the goldeneye duck *Bucephala clangula*. Journal of Animal Ecology 53: 679–692.

Dugger, B. D., K. M. Dugger, and L. H. Fredrickson. 1994. Hooded Merganser *Lophodytes cucullatus*. The birds of North America. Number 98.

Eadie, J. M. 1989. Alternative reproductive tactics in a precocial bird: the ecology and evolution of brood parasitism in goldeneyes. Thesis. University of British Columbia, Vancouver, Canada.

Eadie, J. M. and G. Gauthier. 1985. Prospecting for nest sites by cavity-nesting ducks of the genus *Bucephala*. Condor 87:528–534.

Eadie, J. M., M. L. Mallory, and H. G. Lumsden. 1995. Common Goldeneye *Bucephala clangula*. The birds of North America. Number 170.

Eriksson, M. O. G. 1979. Clutch size and incubation efficiency in relation to nest-box size among goldeneyes *Bucephala clangula*. Ibis 121:107–109.

Eriksson, M. O. G. and M. Andersson. 1982. Nest parasitism and hatching success in a population of goldeneyes *Bucephala clangula*. Bird Study 29: 49–54.

Erskine, A. J. 1990. Joint laying in *Bucephala* ducks—"parasitism" or nest-site competition? Ornis Scandinavica 21:52–56.

Fredga, S. and H. Dow. 1984. Factors affecting the size of a local population of goldeneye *Bucephala clangula* (L.) breeding in Sweden. Viltrevy 13: 225–255.

Gauthier, G. 1989. The effect of experience and timing on reproductive performance in Buffleheads. Auk 106:568–576.

Gauthier, G. and J. N. M. Smith. 1987. Territorial behaviour, nest-site availability, and breeding density in Buffleheads. Journal of Animal Ecology 56:171–184.

Gilmer, D. S., I. J. Ball, L. M. Cowardin, J. E. Mathisen, and J. H. Riechmann. 1978. Natural cavities used by Wood Ducks in north-central Minnesota. Journal of Wildlife Management 42: 288–298.

Haramis, G. M. and D. Q. Thompson. 1985. Density-production characteristics of box-nesting Wood Ducks in a northern greentree impoundment. Journal of Wildlife Management 49:429–436.

Lumsden, H. G., R. E. Page, and M. Gauthier. 1980. Choice of nest boxes by Common Goldeneyes in Ontario. Wilson Bulletin 92:497–505.

Lumsden, H. G., J. Robinson, and R. Hartford. 1986. Choice of nest boxes by cavity-nesting ducks. Wilson Bulletin 98:167–168.

Maisonneuve, C., R. McNicoll, A. Desrosiers, and G. Lupien. 2002. Caractérisation de l'habitat de reproduction des canards arboricoles. Société de la faune et des parcs du Québec, Direction de la recherche sur la faune et Direction de l'aménagement de la faune du Saguenay-Lac Saint-Jean, Quebec City, Quebec, Canada.

Mallory, M. L., H. G. Lumsden, and R. A. Walton. 1993a. Nesting habits of Hooded Mergansers *Mergus cucullatus* in northeastern Ontario. Wildfowl 44:101–107.

Mallory, M. L., D. K. McNicol, and P. J. Weatherhead. 1994. Habitat quality and reproductive effort of Common Goldeneyes nesting near Sudbury, Canada. Journal Wildlife Management 58: 552–560.

Mallory, M. L., D. K. McNicol, R. A. Walton, and M. Wayland. 1998. Risk-taking by incubating Common Goldeneyes and Hooded Mergansers. Condor 100:694–701.

Mallory, M. L., A. Taverner, B. Bower, and D. Crook. 2002. Wood Duck and Hooded Merganser breeding success in nest boxes in Ontario. Wildlife Society Bulletin 30:301–316.

Mallory, M. L., P. J. Weatherhead, D. K. McNicol, and M. E. Wayland. 1993b. Nest site selection by Common Goldeneyes in response to habitat features influenced by acid precipitation. Ornis Scandinavica 24:59–64.

McNicol, D. K., R. A. Walton, and M. L. Mallory. 1997. Monitoring nest box use by cavity-nesting ducks on acid-stressed lakes in Ontario, Canada. Wildlife Biology 3:1–12.

Morse, T. E., J. L. Jakabosky, and V. P. McCrow. 1969. Some aspects of the breeding biology of the Hooded Merganser. Journal of Wildlife Management 33:596–604.

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70:265–276.

Nilsson, S. G. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. Auk 103: 432–435.

Pöysä, H. 1999. Conspecific nest parasitism is associated with inequality in nest predation risk in the Common Goldeneye (*Bucephala clangula*). Behavioural Ecology 10:533–540.

Pöysä, H. and S. Pöysä. 2002. Nest-site limitation and density dependence of reproductive output in the Common Goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. Journal of Applied Ecology 39:502–510.

Pöysä, H., M. Milonoff, V. Ruusila, and J. Virtanen. 1999. Nest-site selection in relation to habitat edge: experiments in the Common Goldeneye. Journal of Avian Biology 30:79–84.

Pöysä, H., P. Runko, V. Ruusila, and M. Milonoff. 2001. Identification of parasitized nests by using egg morphology in the Common Goldeneye: an alternative to blood sampling. Journal of Avian Biology 32:79–82.

Prince, H. H. 1968. Nest sites used by Wood Ducks and Common Goldeneyes in New Brunswick. Journal of Wildlife Management 32:489–500.

Research Unit for Wildlife Assessment. 1999. DISTANCE. Version 3.5. University of St. Andrews, Fife, Scotland.

Salter, K. C. and R. F. Fawcett. 1993. The ART test of interaction: a robust and powerful rank test of interaction in factorial models. Communications in Statistics: Simulation and Computation 22:137–153.

SAS Institute. 1999. SAS/STAT user's guide. Version 8.0. SAS Institute Inc., Cary, North Carolina, USA.

Savard, J.-P. L. 1984. Territorial behaviour of Common Goldeneye, Barrow's Goldeneye and Bufflehead in areas of sympatry. Ornis Scandinavica 15: 211–216.

Savard, J.-P. L. 1988. Use of nest boxes by Barrow's Goldeneyes: nesting success and effect on the breeding population. Wildlife Society Bulletin 16: 125–132.

SEMEL, B. AND P. W. SHERMAN. 2001. Intraspecific parasitism and nest-site competition in Wood Ducks. Animal Behaviour 61:787–803.

SEMEL, B., P. W. SHERMAN, AND S. M. BYERS. 1988. Effects of brood parasitism and nest-box placement on Wood Duck breeding ecology. Condor 90:920–930.

SEMEL, B., P. W. SHERMAN, AND S. M. BYERS. 1990. Nest boxes and brood parasitism in Wood Ducks: a management dilemma. Pages 163–170 *in* Proceedings of the 1988 North American Wood Duck Symposium (L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby, and T. S. Taylor, Editors). St. Louis, Missouri, USA.

SÉNÉCHAL, H. 2003. Étude comparative de l'écologie de nidification et d'élevage des couvées de Garrot à œil d'or (*Bucephala clangula*) et de Harle couronné (*Lophodytes cucullatus*) dans un habitat de rivière. Thesis. Université Laval, Quebec, Canada.

The Wilson Journal of Ornithology 120(4):743–754, 2008

MOVEMENTS AND HABITAT USE BY RED-BREASTED MERGANSER BROODS IN EASTERN NEW BRUNSWICK

SHAWN R. CRAIK[1,2] AND RODGER D. TITMAN[1]

ABSTRACT.—Red-breasted Mergansers (*Mergus serrator*) commonly breed in estuaries, but little is known about their brood-rearing in coastal environments. We measured daily movements and habitat use of radio-marked (n = 17) female Red-breasted Mergansers with broods originating from coastal barrier islands at Kouchibouguac National Park, New Brunswick, Canada from 2002 to 2004. Primary brood movements from nest sites to initial rearing areas were often extensive, averaging 3.5 km (n = 15), since many broods crossed Saint-Louis Lagoon to continental rearing sites. Broods remained mobile throughout the rearing period and there was little difference in daily movements between age class I (days 1–10 post nest exodus), class II (days 11–20), and class III (>20 days) broods. Broods frequented shallow ($\bar{x}$ = 51 cm, 95% CI: 44–58 cm, n = 191 locations), nearshore ($\bar{x}$ = 47 m, 95% CI: 33–60 m, n = 157 locations) waters that often supported submergent eel grass (*Zostera marina*). Broods selected estuarine intertidal regions in Saint-Louis and Kouchibouguac lagoons, as well as wetlands at the mouths of tidal streams. Few broods were found in tidal river and marine habitats. Continental estuarine intertidal, tidal stream, and saltmarsh habitats were preferred by age class I broods whereas estuarine intertidal and subtidal habitats were preferred by age classes II and III. This study highlights the importance of estuarine habitats in lagoons and tidal streams for brood-rearing Red-breasted Mergansers in eastern New Brunswick. *Received 22 June 2007. Accepted 31 January 2008.*

Adult waterfowl may enhance juvenile recruitment by assisting young in locating suitable habitats throughout the brood-rearing period (Afton and Paulus 1992). Parents select wetlands where food quality and abundance are greatest to meet the nutritional requirements of developing young (Minot 1980, Talent et al. 1982), and use areas that provide loafing sites for resting broods (Bengtson 1971b). Movements and habitat selection by brood-rearing females have been documented for a variety of dabbling (Anatini) and diving (Aythyini) duck species, including Mallard (*Anas platyrhynchos*) (Krapu et al. 2006), Wood Duck (*Aix sponsa*) (Granfors and Flake 1999), Redhead (*Aythya americana*) (Yerkes 2000a, b), and Canvasback (*Aythya valisineria*) (Austin and Serie 1991). Few studies have investigated daily movements and patterns of brood habitat selection by sea ducks (Mergini) breeding at inland and, in particular, at coastal sites, despite this tribe representing over 40% of duck species breeding in North America (Palmer 1976, Pöysä and Virtanen 1994). The brood-rearing activities of many sea duck populations are poorly known because sea ducks often breed at low densities across remote areas where studies are logistically difficult (Décarie et al. 1995). Characterization of important breeding sites is needed given increased concern about population declines of many species of sea ducks (Sea Duck Joint Venture Management Board, unpub. data).

The Red-breasted Merganser (*Mergus serrator*) has a Holarctic distribution and is a common breeder on fresh and saltwater wetlands (Titman 1999). The breeding population of Red-breasted Mergansers in the Canadian Maritime Provinces was estimated at 7,500 birds, many of which occur colonially in estuaries throughout eastern New Brunswick (Erskine 1992, Titman 1999). Little is known about movements and habitat use of merganser broods occurring at these coastal sites, which consist of a variety of estuarine and marine habitats. Information regarding movements and habitat use by Red-breasted Merganser broods is restricted to the Palearctic freshwaters of Iceland where Bengtson (1971b) studied movements of newly-hatched young and documented general distribution of broods at Lake M'yvatn.

Brood movements from nest sites to initial rearing habitats (primary movements) and subsequent movements to alternate areas (secondary movements) generally indicate that waterfowl broods actively select habitats throughout the rearing period (Mauser et al.

[1] Department of Natural Resource Sciences, McGill University, Ste-Anne-de-Bellevue, QC H9X 3V9, Canada.

[2] Corresponding author; e-mail: shawn.craik@mail.mcgill.ca

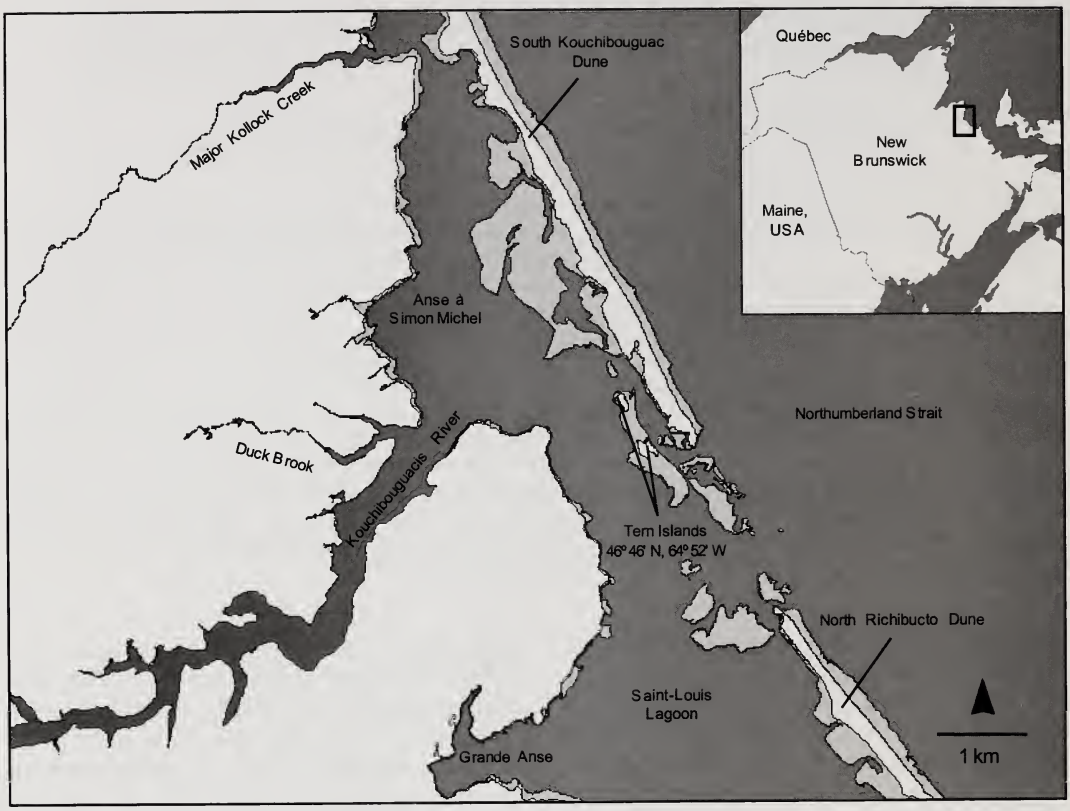


FIG. 1. Study site at Kouchibouguac National Park, New Brunswick, Canada, 2002–2004. Red-breasted Merganser brood-rearing sites included Grande Anse, Anse à Simon Michel, Major Kollock Creek, and Duck Brook. Light shaded regions indicate intertidal flats.

1994, Granfors and Flake 1999). Habitat use may vary with brood age and result from varying physiological, nutritional, and behavioral requirements of young waterfowl from hatching to fledging (Berg 1956, Beard 1964, Rotella and Ratti 1992).

We investigated movements and patterns of habitat selection by Red-breasted Merganser broods occurring in a saltwater environment, focusing on broods that originated from a merganser nesting colony in New Brunswick, Canada. Specific objectives were to: (1) measure distances traveled to initial brood-rearing locations and to subsequent rearing locations; (2) examine patterns of habitat use relative to availability; and (3) examine brood-age related changes in daily movements and habitat use.

METHODS

Study Area.—Work was conducted from late May to mid-September 2002 to 2004 at Kouchibouguac National Park, New Brunswick, Canada (46° 46′ N, 64° 52′ W) (Fig. 1). The park occupies an area of 239 km^2 on the coast of the Magdalene Shallows Natural Marine Region; the marine waters of Northumberland Strait are separated from an estuary by a 26-km crescent of barrier islands. The estuary consists of Saint-Louis and Kouchibouguac lagoons, and the tidal regions of several rivers and streams, including the Kouchibouguacis and Kouchibouguac rivers and Major Kollock Creek (Fig. 1). Eelgrass (*Zostera marina*) occurred over shallows of much of the area (salinity >7%), but widgeon grass (*Ruppia maritima*) dominated brackish waters (Beach 1988). Average water depths in the estuary were shallow (<1 m) except for several channels (2–6 m) and over unvegetated intertidal flats (0.3 m) (Beach 1988). Saltmarsh, consisting of two zones, fringed much of the continental side of the lagoons. The low

marsh was flooded daily by tides (<0.7 m tidal amplitude) and was dominated by saltwater cordgrass (*Spartina alterniflora*), whereas the upper marsh was only infrequently flooded by the highest tides and saltmeadow cordgrass (*Spartina patens*), saltmarsh sedge (*Carex paleacea*), and prairie cordgrass (*Spartina pectinata*) were most common (Beach 1988).

Red-breasted Mergansers nested colonially on Tern Islands, a 2.8-ha island complex consisting of three barrier islands in Saint-Louis Lagoon (Fig. 1). The islands are composed of sand and primarily stabilized by marram grass (*Ammophila breviligulata*). Potential duckling predators included Great Black-backed (*Larus marinus*) and Herring (*L. argentatus*) gulls, American Crows (*Corvus brachyrhynchos*), Common Ravens (*C. corax*), Northern Harriers (*Circus cyaneus*), and red fox (*Vulpes vulpes*).

Data Collection.—Merganser nests were located each year by systematically searching Tern Islands on foot between 0700 and 1100 hrs AST once a week from late May to early July. Nest coordinates were obtained using a global positioning system (GPS) with 4 m accuracy (model eTrex, Garmin Ltd., Olathe, KS, USA). Hatching date was estimated for each nest by floating 2–3 incubated eggs in water and assuming an incubation period of 30 days (Westerskov 1950). Females were captured on the nest during the last week of incubation using a dip net or automatic nest trap (Weller 1957), and were equipped with radio transmitters subcutaneously implanted immediately posterior to the nape (model PD-2, Holohil Systems Ltd., Carp, ON, Canada) (Korschgen et al. 1996). Transmitters weighed between 3.1 and 3.8 g, which represented <0.6% of the total body mass of the lightest marked female (680 g). Females were captured and radiomarked throughout the hatching season (early Jul-early Aug).

We attempted to locate marked broods (hen and ≥1 duckling) once daily post-nest exodus (White and Garrott 1990). Locations were obtained throughout the diurnal period (0600–2100 hrs) for each brood from a sea kayak; however, a small motorboat (3 m) was occasionally used. Efforts were made to monitor broods to 45 days post-nest exodus, after which brood-hen bonds generally deteriorated. Total brood mortality or abandonment was assumed when a marked hen was observed post-nest exodus either alone or with other female mergansers. We excluded travel locations between rearing sites (n = 2) and locations that may have been influenced by our activity (n = 8). We assumed investigator disturbance occurred when broods were initially spotted swimming directly away from the boat. Efforts were made upon obtaining a telemetry signal from a brood to observe the brood with binoculars from as great a distance as possible (>500 m). This was feasible given the open environment and often linear shorelines of the estuarine and marine habitats at Kouchibouguac. We approached brood locations only when broods had moved >200 m to further reduce the possibility of investigator influence on brood movements.

We recorded coordinates (location of brood where initially observed) at each location with a GPS and broods were classified to age class as: (I) days 1–10 post nest exodus, (II) days 11–20, and (III) >20 days (Austin and Serie 1991). We measured water depth (cm) and distance to shore (m) at each location, and estimated proportion of cover of three submergent vegetation types (eelgrass, widgeon grass, macro algae) within a 5-m radius centered on the location.

Habitat Map.—Coastal habitat types within the study area were delineated with use of the Wetlands of the Maritime Provinces classification system (Hanson and Calkins 1996). Habitats were classified as: (1) tidal river, (2) tidal stream (1–3 order), (3) saltmarsh, (4) estuarine intertidal flat in the lagoons, (5) estuarine subtidal flat in the lagoons, (6) marine intertidal flat, and (7) marine subtidal flat. We divided estuarine intertidal flat into continental estuarine intertidal and barrier island estuarine intertidal. Estuarine intertidal habitats were distinguished from estuarine subtidal by the absence of extensive eelgrass meadows at intertidal areas (Hanson and Calkins 1996). Marine intertidal habitat included nearshore, foreshore, and backshore regions (Godfrey 1976). We excluded barrier island and upland habitats (forests, freshwater wetlands) from analyses given complete avoidance of these habitats by merganser broods. Candidate habitats (n = 8) were identified on a mosaic of digital geo-referenced orthophotographs provided by Parks Canada and habitats were dig-

itized from the mosaic using Cartalinx 1.04 (Clark Laboratories, Worcester, MA, USA).

Data Analyses.—Primary and secondary movements for each brood were measured as straight-line distances (km) using ArcView GIS 3.1 (Environmental Systems Research Institute Inc., Redland, CA, USA). Secondary movements were calculated only when a brood was located on consecutive days. Movement data were summarized by pooling locations among broods so that daily movements were compared between each of the three brood age classes. Data were square-root transformed to improve normality (Shapiro-Wilk Test = 0.95) prior to a one-way analysis of variance (ANOVA). We defined a home range as the area where broods restricted their activities during observation (Mauser et al. 1994). Home range size (ha) was calculated for broods that were assumed to have fledged at least one duckling (≥13 locations) using the minimum convex polygon (MCP) method with the Animal Movement Program 2.0 (Hooge and Eichenlaub 2000) in ArcView. Before estimating home ranges, 5% of outlying locations were removed from each brood using the harmonic mean method (Dixon and Chapman 1980). We measured the total distance moved (km) throughout the observation period for these broods.

Habitat use by broods was compared to availability at two spatial scales (Johnson 1980). First, proportions of each habitat within brood home ranges were compared to those available (second-order selection). Second, we compared proportions of telemetry locations that occurred in each habitat type to those within home ranges (third-order selection). Habitat availability was calculated for each brood by creating a thematic map in ArcView containing used habitats surrounding the nest within a radius equivalent to the distance between a brood's nest and its farthest location from the nest (Granfors and Flake 1999, Chouinard and Arnold 2007). The thematic map was clipped in the habitat map to estimate the proportion of each habitat type available to individual broods. Thematic maps containing brood home ranges were also clipped in the habitat map to estimate the proportion of each habitat type that occurred within individual home ranges. Telemetry locations were overlaid onto the habitat map to estimate the proportion of locations that occurred within each habitat for each brood.

The Friedman (1937) ranking procedure was used for each brood to examine trends in differences in availability and use of each habitat type across broods, which resulted in habitats being ranked from one to eight at the second and third orders of selection. Compositional analysis (CA) was used to examine habitat selection at the two spatial scales (Aebischer et al. 1993, Smith 2003). Habitat proportions with zero values were replaced with 0.00001, a value an order of magnitude smaller than the smallest non-zero value used or available, to calculate log-ratios (Aebischer et al. 1993). Randomization procedures were used to avoid inflated Type I error rates produced by CA (Bingham and Brennan 2004, Thomas and Taylor 2006). We generated 2,500 data sets of the same size (number of broods) and number of locations as the original data but under the hypothesis of random habitat use (Pendleton et al. 1998, Granfors and Flake 1999). A matrix of *t*-tests was constructed if nonrandom selection of habitats occurred ($P < 0.05$) by using differences of log-ratios between habitats of interest to rank habitat preferences and examine where ranks differed (Aebischer et al. 1993). Broods tracked for fewer days provided less information, thus, observations were weighted by the square-root of the number of days observed (Granfors 1996). We considered broods that were assumed to have fledged young ($n = 6$) or were observed on at least eight occasions ($n = 2$) prior to total brood mortality or brood abandonment for analyses of habitat selection.

Effects of brood age on habitat use were evaluated using a Chi-square goodness of fit test for each of the three brood-age classes (White and Garrott 1990). Few broods ($n = 6$) provided information about each age class and many broods had few locations (<6) within a given age class, thus, locations were pooled among broods and assigned to one age class (Alldredge and Ratti 1986, Gammonley 1990). Available habitat was estimated by creating a thematic map in ArcView containing used habitats surrounding the nest of the brood with the largest radius between the brood's nest and its farthest location from the nest. The thematic map was clipped in the habitat map to calculate the proportion of each

habitat type available. Brood locations were overlaid onto the habitat map to calculate the proportion of locations that occurred within each habitat for each age class. We used an exact test to compare use of habitats within each age class because of many small expected frequencies (<5) in the Chi-square table (Sokal and Rohlf 1981). Bonferroni confidence intervals were calculated if nonrandom selection occurred within an age class ($P < 0.05$) to identify which habitat types were preferred or avoided (Byers and Steinhorst 1984). Data analyses were conducted using SPSS 11.5 (SPSS Inc., Chicago, IL, USA) and SAS 9.1 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Marking and Tracking.—Twenty-seven female mergansers were fitted with transmitters. Nests of three marked females were unsuccessful, and location data were unavailable for three females without broods post-nest exodus and four females that were not found following nest exodus. We obtained 233 locations ($\bar{x}$ = 13.7 locations/brood, range 1 to 45) from 17 broods. The mean brood age at last observation was 16.2 days post-nest exodus and ranged from 0 to 51 days (day 0 = day of nest exodus). Ninety (38%) locations were recorded for age class I broods, 49 (21%) for class II broods, and 95 (41%) for class III broods.

Movements.—Primary movements averaged 3.5 km (95% CI: 2.8–4.2 km, n = 15) and ranged from 0.6 to 5.9 km. Most broods crossed Saint-Louis Lagoon from Tern Islands to the continent and subsequently traveled north or south along shorelines to estuarine bays or mouths of tidal streams. One hen in 2003 led her brood <1 km from her nest to initial rearing habitat along the shorelines of Tern Islands. One female, marked in both 2003 and 2004, led her broods to Anse à Simon Michel, a shallow bay in Saint-Louis Lagoon, in both years (Fig. 1).

Secondary movements averaged 1.0 km/day (95% CI: 0.8–1.2 km, n = 157 locations) and ranged from localized movements (<0.1 km) to 7.9 km. Secondary movements were typically not directional (consistently moving away from Tern Islands) as broods often returned to previous rearing sites. Overall, brood movements were greatest immediately post-nest exodus (Table 1), but there were no differences in average daily movements between age class I, class II, and class III broods ($F_{2,202}$ = 0.48, P = 0.62). Mean home range was 806 ha (95% CI: 40–1,572 ha) and ranged from 196 to 2,199 ha for those broods that were assumed to have fledged young (n = 6). Total distance traveled by these broods averaged 44.0 km (95% CI: 20.2–67.7 km) and ranged from 17.4 to 81.2 km.

TABLE 1. Distances moved by Red-breasted Merganser broods for three age classes at Kouchibouguac National Park, New Brunswick, 2002–2004.

Age class[a]	Mean distance moved/day (km)	95% CI (km)	Range (km)	Broods[b]	Observations
I	1.3	1.0–1.7	0.0–5.9	15	76
II	1.1	0.7–1.4	0.1–7.9	5	52
III	1.1	0.9–1.3	0.0–3.5	6	77

[a] I = days 1–10 post-nest exodus, II = days 11–20, III = >20 days.
[b] Number of broods that provided movement data within each brood age class.

Microhabitat.—Microhabitat at brood locations varied by habitat type (Table 2). Overall, broods frequented shallow waters ($\bar{x}$ = 51 cm, 95% CI: 44–58 cm, n = 191 locations) near shorelines ($\bar{x}$ = 47 m, 95% CI: 33–60 m, n = 157 locations). The proportion of submergent vegetation at locations averaged 38.3% (95% CI: 33.8–42.9%, n = 212 locations). Eelgrass occurred at 84.7% of 216 brood locations whereas macro algae and widgeon grass each occurred at <20% of locations. Eelgrass cover at brood locations was considerably higher ($\bar{x}$ = 35.2%, 95% CI: 30.8–39.4%, n = 216 locations) than that of macro algae ($\bar{x}$ = 3.4%, 95% CI: 1.9–4.9%, n = 216 locations) or widgeon grass ($\bar{x}$ = 0.6%, 95% CI: 0–1.3%, n = 216 locations) (χ^2 = 299.49, df = 2, $P < 0.001$).

Broods loafed on shore typically <1 m from water. Broods on the continental side of lagoons rested on sandy intertidal areas surrounded by saltwater cordgrass and on peat deposits consisting of scattered cordgrass. Broods on the barrier island side of lagoons loafed on intertidal beaches that lacked vegetative concealment.

Habitat Use and Selection.—We observed little variability across broods when differences of availability and use for each habitat were examined (Table 3). Estuarine subtidal was

TABLE 2. Habitat characteristics at Red-breasted Merganser brood locations within four habitat types at Kouchibouguac National Park, New Brunswick, 2002–2004. Data were obtained from 17 broods.

	Habitat type[a]			
	STR	ES	IFB	IFC
Mean water depth, cm	30.3	65.3	38.2	33.3
95% CI	20.4–40.2	52.7–77.8	24.9–51.3	27.2–39.5
Range	4.9–64.1	2.7–475.0	2.2–122.6	2.0–91.8
n	20	86	20	46
Mean distance to shore, m	22.0	77.5	13.3	16.0
95% CI	6.3–37.7	53.5–101.3	7.6–18.9	12.4–19.7
Range	2.1–45.3	0.9–771.0	0.3–39.2	0.1–45.1
n	7	80	22	41
Mean vegetative cover, %[b]	33.8	44.4	20.2	36.7
95% CI	20.5–47.0	37.5–51.3	7.4–33.0	28.0–45.4
Range	5.0–95.0	0.0–100	0.0–100	0.0–100
n	20	94	24	55
Occurrence, %[b]				
Eelgrass	100 (20/20)	89.4 (84/94)	65.2 (15/23)	84.9 (45/53)
Macro algae[c]	30.0 (6/20)	7.4 (7/94)	13.0 (3/23)	9.4 (5/53)
Widgeon grass	15.0 (3/20)	2.1 (2/94)	0.0 (0/23)	3.8 (2/53)
Cover, %[b]				
Eelgrass				
Mean	26.3	42.8	18.1	33.4
95% CI	17.0–35.5	35.9–49.8	6.4–29.8	25.5–41.3
Range	5.0–70.0	0.0–100	0.0–100	0.0–100
n	20	94	24	55
Macro algae[c]				
Mean	5.8	0.9	2.1	3–4
95% CI	0.0–12.6	0.0–1.8	0.0–5.5	0.7–6.1
Range	0.0–50.0	0.0–40.0	0.0–40.0	0.0–50.0
n	20	94	24	55
Widgeon grass				
Mean	1.8	0.3	0.0	0.0
95% CI	0.0–3.7	0.0–0.7		
Range	0.0–15.0	0.0–20.0		
n	20	94	24	55

[a] STR = tidal stream, ES = estuarine subtidal, IFB = barrier island estuarine intertidal, and IFC = continental estuarine intertidal. Other habitats excluded since few locations (≤6) were available.
[b] Measured within a 5-m radius centered on brood location. Included live and dead vegetation.
[c] Families Phaeophyta, Rhodophyta, Cyanophyta, and Chlorophyta.

ranked first (most used) for all eight broods at the second order of selection and continental estuarine intertidal was ranked either first or third for all broods at the third order of selection (Table 3). Use of habitats was proportional to availability at the second order of selection (Wilk's $\lambda = 0.002$, $\chi^2 = 50.79$, df = 7, randomized $P = 0.26$). However, marine ($n = 5$ locations) and river ($n = 4$ locations) habitats were generally not important to brood home ranges (Table 4), and all river locations were within 2.8 km of a lagoon.

Marine and tidal river habitats were excluded from analyses of third-order selection as at least six non-missing log-ratio differences, necessary for randomization to show a difference from zero at $P < 0.05$ (df ≥ 5 for *t*-tests), were unavailable. Removal of habitats did not affect ranking among remaining habitats. Habitat use was nonrandom (weighted mean Wilk's $\lambda = 0.13$, $\chi^2 = 16.51$, df = 4, randomized $P = 0.03$) at the third order of selection (Table 4). Continental estuarine intertidal was ranked first but was not used more ($P = 0.52$) than tidal stream. Broods used shallow intertidal areas in several continental bays, including Anse à Simon Michel and Grande Anse, and at the mouths of tidal

TABLE 3. Habitat ranks for eight Red-breasted Merganser broods at Kouchibouguac National Park, New Brunswick, 2002-2004. Ranks calculated at the second and third orders of habitat selection. Numbers in parentheses represent number of locations.

	Habitat type[a]							
Brood ID	STR	ES	IFB	IFC	MI	MS	RIV	SM
150 (n = 39)	5/2[b]	1/6	2/5	4/1	6/n	8/n	7/3	3/4
131 (n = 13)	6/2	1/7	3/1	5/3	2/4	8/6	7/n	4/5
711 (n = 8)	4/2	1/5	7/4	2/1	5/n	8/n	6/n	3/3
638 (n = 29)	4/n	1/6	2/1	5/3	3/2	8/4	6/n	7/5
500 (n = 38)	5/3	1/6	2/4	4/1	7/n	8/n	6/2	3/5
209 (n = 22)	5/3	1/7	2/6	3/1	6/5	8/n	7/4	4/2
529 (n = 31)	5/2	1/8	2/6	4/1	7/4	8/3	6/5	3/7
120 (n = 8)	4/2	1/3	7/n	3/1	5/n	8/n	6/n	2/4

[a] STR = tidal stream, ES = estuarine subtidal, IFB = barrier island estuarine intertidal, IFC = continental estuarine intertidal, MI = marine intertidal, MS = marine subtidal, RIV = tidal river, and SM = saltmarsh.

[b] 5/2, where 5 is habitat rank (observed − expected frequencies) at second order of selection and 2 is rank at third order of selection. Rank of 1 = most used. (n) denotes no rank since habitat was not available.

streams, such as Major Kollock Creek and Duck Brook (Fig. 1). Brood locations that occurred in streams were near stream mouths (<675 m) that emptied into the lagoons. Estuarine subtidal was ranked last and was used less (P = 0.008) than continental estuarine intertidal and barrier island estuarine intertidal (P = 0.02). The relatively little use of estuarine subtidal reflected large areas of deep (>75 cm), offshore (>100 m) subtidal habitat that was not used in brood home ranges. Most broods regularly used shallow, nearshore estuarine subtidal habitats (Table 4).

Use of habitats was nonrandom for brood age class I (χ^2 = 1,318.03, df = 7, P < 0.001). Continental estuarine intertidal, tidal stream, and saltmarsh habitats were preferred (Table 5). Habitat use was also nonrandom for brood age classes II (χ^2 = 452.21, df = 7, P < 0.001) and III (χ^2 = 1,723.03, df = 7, P < 0.001) as continental estuarine intertidal, barrier island estuarine intertidal, and estuarine subtidal habitats were preferred for these age classes (Table 5).

DISCUSSION

Movements.—Distances traveled by Red-breasted Merganser broods from nests on Tern Islands to rearing areas were variable but often exceeded 3 km. Extensive travels are common for waterfowl broods moving from nesting islands to continental wetlands (Munro and Bédard 1977, Sayler and Willms 1997). In Lake Michigan, Braun et al. (1980) report-

TABLE 4. Mean (± 95% CI) percentages of available habitats, habitats within home ranges, and habitats at locations for eight Red-breasted Merganser broods at Kouchibouguac National Park, New Brunswick, 2002–2004 (n = 188 locations).

	Habitat type[a]							
	STR	ES	IFB	IFC	MI	MS	RIV	SM
Available	0.4 ± 0.1	24.0 ± 6.2	4.2 ± 2.1	1.0 ± 0.1	1.4 ± 0.3	62.8 ± 8.1	2.5 ± 0.6	3.8 ± 0.8
Home range	0.6 ± 0.5	65.9 ± 13.7	10.7 ± 6.2	6.0 ± 5.9	3.0 ± 2.5	4.5 ± 10.7	0.9 ± 1.1	9.9 ± 6.5
Locations	11.0 ± 11.0	26.1 ± 17.8	17.7 ± 15.9	29.4 ± 11.8	0.9 ± 2.0	2.9 ± 6.8	2.1 ± 2.9	9.9 ± 8.1
Rank: 2nd order[b]	N/A							
Rank: 3rd order[c]	IFC > STR > IFB > SM > ES[d]							

[a] STR = tidal stream, ES = estuarine subtidal, IFB = barrier island estuarine intertidal, IFC = continental estuarine intertidal, MI = marine intertidal, MS = marine subtidal, RIV = tidal river, and SM = saltmarsh.

[b] Home ranges vs. available habitat. Randomized P = 0.26 and habitats were not ranked.

[c] Telemetry locations vs. home ranges. Habitats are presented in rank order where they are separated with > symbols, those to the left being of higher rank than those to the right. Habitats that share an underline were used equally (P > 0.05).

[d] Randomization indicated greater (P = 0.02) use of IFB in comparison to ES.

TABLE 5. Characteristics of available habitats for three age classes of Red-breasted Merganser broods at Kouchibouguac National Park, New Brunswick, 2002–2004. Data were obtained from 17 broods.

	Habitat type[a]							
	STR	ES	IFB	IFC	MI	MS	RIV	SM
Clss I[b]								
# of locations	18	19	8	18	0	0	4	16
% of locations	0.22	0.23	0.10	0.22	0	0	0.05	0.19
Bonferroni CI	0.09–0.34	0.10–0.36	0.01–0.19	0.09–0.34	0–0.001	0–0.001	0–0.02	0.07–0.31
Preferred/Avoided[c]	Preferred	—	—	Preferred	—	Avoided	—	Preferred
Class II[b]								
# of locations	2	16	16	22	0	0	2	3
% of locations	0.05	0.36	0.23	0.25	0	0	0.05	0.07
Bonferroni CI	0–0.13	0.17–0.56	0.05–0.40	0.07–0.43	0–0.001	0–0.001	0–0.13	0–0.17
Preferred/Avoided	—	Preferred	Preferred	Preferred	—	Avoided	—	—
Class III[b]								
# of locations	1	26	19	33	2	3	1	2
% of locations	0.49	0.30	0.22	0.38	0.02	0.03	0.01	0.02
Bonferroni CI	0–0.11	0.17–0.43	0.10–0.34	0.24–0.52	0–0.07	0–0.09	0–0.11	0–0.07
Preferred/Avoided	—	Preferred	Preferred	Preferred	—	Avoided	—	—
% available	0.01	0.15	0.02	0.01	0.01	0.75	0.04	0.02

[a] STR = tidal stream, ES = estuarine subtidal, IFB = barrier island estuarine intertidal, IFC = continental estuarine intertidal, MI = marine intertidal, MS = marine subtidal, RIV = tidal river, and SM = saltmarsh.
[b] Class I = days 1–10 post-nest exodus; Class II = days 11–20; Class III = >20 days.
[c] (−) denotes no preference or avoidance for habitat type.

ed travel by a Red-breasted Merganser brood of nearly 1 km from its nesting island to rearing habitat along the continent. Primary movements by Common Eider (*Somateria mollissima*) broods may exceed 10 km toward continental rearing areas (Munro and Bédard 1977).

Movements to the continent by newly-hatched merganser broods may have been necessary if suitable brood-rearing conditions did not occur near the nesting islands. Predation pressure on broods was likely higher along barrier islands since Great Black-backed and Herring gulls were more common around Tern Islands than the continent. Young and Titman (1986) suggested that merganser duckling survival at Kouchibouguac may have been reduced by the numerous gulls along North Richibucto Dune (~1 km south of Tern Islands) and that broods moved quickly from island nests to continental shorelines, possibly to avoid predation. Predation pressure by gulls was likely higher during Young and Titman's (1986) study than in 2002–2004 when <5 nests and small numbers of gulls were observed on Tern Islands. However, as many as 500 gull nests occurred annually on Tern Islands during the late 1990s (Robert Ouellette, pers. comm.).

Daily movements by merganser broods were most extensive within 10 days post-nest exodus (age class I), which likely reflected movements from nest sites. Movements of this age class were greater in our study than those reported at Lake M'yvatn, Iceland, where daily travel by newly-hatched broods averaged 265 m and ranged from 160 to 3,400 m (Bengtson 1971b). Bengtson (1971b) was not able to follow broods throughout the entire rearing period but merganser broods at Kouchibouguac generally remained highly mobile in age classes II and III, often traveling >1 km/day. This mobility may be linked to foraging since mergansers are very mobile while searching for small fish (Wood 1985), often using extensive paths along shorelines in search of prey (Wood and Hand 1985). Merganser broods may move large distances in search of prey, particularly when previous sites are unprofitable (Wood 1985).

Multiple merganser broods often occupied nearby loafing and foraging sites, which suggested that encounters between broods were likely common. It was generally unknown whether brood movements were triggered by agonistic behavior between broods, but on 22 August 2004, an amalgamated brood of 23 young was aggressively displaced from the mouth of Major Kollock Creek by the hen of an older brood of 7 young. Aggression between brood-rearing female Red-breasted Mergansers was reported in Denmark but there was no indication these behaviors resulted in brood movements (Kahlert 1993).

We eliminated brood locations that were apparently influenced by investigator activity (e.g., boat tracking). However, our activities may have resulted in undetected brood displacement on a small number of occasions, such as during motorboat departures from brood locations following habitat measurements. Fast-moving motorboats in Denmark were twice as likely to disturb merganser broods than smaller boats, but these broods quickly resumed their activities once the disturbance had passed (Kahlert 1993). It is unlikely that our tracking efforts had a major role in affecting brood movements, given that disturbed broods did not move large distances (>200 m) and that some broods made extensive secondary movements (>2 km) regardless of whether they were followed by kayak or motorboat.

Habitat Use and Selection.—Merganser broods predominantly used shallow, nearshore intertidal and subtidal estuarine habitats throughout Saint-Louis and Kouchibouguac lagoons. Several broods also used the mouths of tidal streams that emptied into the lagoons. These habitats provided an abundance of small fish throughout the brood-rearing period. Threespine (*Gasterosteus aculeatus*), blackspotted (*G. wheatlandi*), fourspine (*Apeltes quadracus*), and ninespine (*Pungitius pungitius*) sticklebacks, mummichog (*Fundulus heteroclitus*), Atlantic silverside (*Menidia menidia*), and cunner (*Tautogolabrus adspersus*) were common in the lagoons throughout summer and represented much of the total fish biomass present within the park's estuarine system (Klassen 2001, Joseph et al. 2006). Broods were observed foraging (n = 36 locations) over stands of submergent eelgrass in shallow (<1 m) subtidal waters near intertidal areas. Eelgrass meadows provide sticklebacks and other small fish with nursery habitat that

generally produces more adult recruits than other juvenile fish habitats (Beck et al. 2001, Joseph et al. 2006).

Habitat selection by mergansers is affected by availability and abundance of fish (Kaminski and Weller 1992). Abundance of Common Merganser (*Mergus merganser*) broods in British Columbia was linked to abundance of juvenile Pacific salmon (*Oncorhyncus* spp.) (Wood 1986) and distribution of Red-breasted Merganser broods is closely related to the distribution and abundance of small fish (<15 cm) (White 1957, Bengtson 1971a, Råd 1980). Sjöberg (1989) suggested the breeding period for Red-breasted Mergansers is synchronized with movements of threespine sticklebacks where broods forage on juvenile fish that move downstream to coastal regions. Sticklebacks were likely the most abundant fish in the lagoons at Kouchibouguac throughout the merganser brood-rearing period (Klassen 2001).

Continental estuarine intertidal, tidal stream, and saltmarsh habitats were preferred by age class I broods. These continental habitats provided newly-hatched broods with shallow waters (<50 cm) that offered shelter from wind and larger waves, which likely improved foraging given the limited diving abilities of young mergansers (Beard 1964). These areas also provided young broods with loafing sites in saltwater cordgrass. Vegetative concealment may have reduced predator detection of age class I broods during a period when duckling mortality is often highest (Flint and Grand 1997, Guyn and Clark 1999). We observed little use of stream and saltmarsh habitats for brood age classes II and III as more open estuarine intertidal and subtidal habitats were used by each of these age classes. Bengtson (1971b) observed young merganser broods in restricted areas near continental and island shorelines whereas older broods occurred in more open areas of Lake M'yvatn. Older merganser broods (>2 weeks) may use deeper, more open habitats since shallow waters and concealment are likely of less importance than for younger broods.

Age-related shifts in habitat use may be influenced by changes in duckling food requirements (Beard 1964, Gammonley 1990, Afton and Paulus 1992). The diet of merganser young at Kouchibouguac has not been documented, so it is not known whether temporal variation in habitat use is influenced by changes in duckling food requirements (Bengtson 1971a) or by variability in distribution and abundance of food resources at brood-rearing sites.

ACKNOWLEDGMENTS

We are grateful to Kouchibouguac National Park, particularly Éric Tremblay and Audrey Beaudet, for providing logistical support. M. J. Bouchard, G. O. Fraser, Mireille Gravel, P.-É. Hébert, L. N. Leger, R. M. Leighton, B. J. Martin, E. J. Reese, E. A. Titman, and especially Amélie Rousseau assisted with data collection. We thank K. P. Kenow for teaching S. R. Craik the transmitter implantation technique and G. O. Fraser for providing sea kayaks. L. A. Egan-Mitton assisted with surgeries. Guillaume Larocque and Bernard Pelletier provided GIS and statistical assistance, respectively. Female capture and transmitter attachment procedures were in compliance with the Canadian Council on Animal Care (CCAC). Funding for this project was provided by Bird Protection Québec, Bishop's University, Canadian Wildlife Federation, and New Brunswick Wildlife Trust Fund. R. G. Clark, C. E. Donehower, M. A. Gahbauer, M.-A. R. Hudson, M. A. J. O'Connor, M. J. Richardson, J.-P. L. Savard, J. T. Ratti, and an anonymous reviewer provided helpful comments on earlier versions of the manuscript.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from radio-tracking data. Ecology 74:1313–1325.

Afton, A. D. and S. L. Paulus. 1992. Incubation and brood care. Pages 62–108 *in* Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Editors). University of Minnesota Press, Minneapolis, USA.

Alldredge, J. R. and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157–165.

Austin, J. E. and J. R. Serie. 1991. Habitat use and movements of Canvasback broods in southwestern Manitoba. Prairie Naturalist 23:223–228.

Beach, H. 1988. The resources of Kouchibouguac National Park: resource description and analysis. Kouchibouguac National Park, Environment Canada, New Brunswick, Canada.

Beard, E. B. 1964. Duck brood behavior at the Seney National Wildlife Refuge. Journal of Wildlife Management 28:492–521.

Beck, M. W., K. L. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001.

The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641.

Bengtson, S.-A. 1971a. Food and feeding of diving ducks breeding at Lake M'yvatn, Iceland. Ornis Fennica 48:77–92.

Bengtson, S.-A. 1971b. Habitat selection of duck broods in Lake M'yvatn area, north-east Iceland. Ornis Scandinavica 2:17–26.

Berg, P. F. 1956. A study of waterfowl broods in eastern Montana with special reference to movements and the relationship of reservoir fencing to production. Journal of Wildlife Management 20:253–262.

Bingham, R. L. and L. A. Brennan. 2004. Comparison of Type I error rates for statistical analyses of resource selection. Journal of Wildlife Management 68:206–212.

Braun, B. M., P. A. Heinz, and G. H. Heinz. 1980. Herring Gull predation on Red-breasted Merganser ducklings. Wilson Bulletin 92:403.

Byers, C. R. and R. K. Steinhorst. 1984. Clarification of a technique for analysis of utilization-availability data. Journal of Wildlife Management 48:1050–1053.

Chouinard, M. P. and T. W. Arnold. 2007. Survival and habitat use of Mallard (*Anas platyrhynchos*) broods in the San Joaquin Valley, California. Auk 124:1305–1316.

Décarie, R., F. Morneau, D. Lambert, S. Carrière, and J.-P. L. Savard. 1995. Habitat use by brood-rearing waterfowl in subarctic Québec. Arctic 48: 383–390.

Dixon, K. R. and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040–1044.

Erskine, A. J. 1992. Atlas of breeding birds of the Maritime Provinces. Nimbus Publishing and Nova Scotia Museum, Halifax, Nova Scotia, Canada.

Flint, P. L. and J. B. Grand. 1997. Survival of Spectacled Eider adult females and ducklings during brood rearing. Journal of Wildlife Management 61:217–221.

Friedman, M. 1937. The use of ranks to avoid the assumption of normality implicit in the analysis of variance. Journal of the American Statistical Association 32:675–701.

Gammonley, J. H. 1990. Habitat use and survival of Wood Duck broods in Mingo Swamp. Thesis. University of Missouri-Columbia, Columbia, USA.

Godfrey, P. J. 1976. Barrier beaches of the East Coast. Oceanus 19:27–40.

Granfors, D. A. 1996. Wood Duck brood movements, habitat use, and survival rates on two prairie rivers in South Dakota. Dissertation. South Dakota State University, Brookings, USA.

Granfors, D. A. and L. D. Flake. 1999. Wood Duck brood movements and habitat use on prairie rivers in South Dakota. Journal of Wildlife Management 63:639–649.

Guyn, K. L. and R. G. Clark. 1999. Factors affecting survival of Northern Pintail ducklings in Alberta. Condor 101:369–377.

Hanson, A. R. and L. Calkins. 1996. Wetlands of the Maritime Provinces: revised documentation for the Wetlands Inventory. Technical Report Number 267. Canadian Wildlife Service, Atlantic Region, Sackville, New Brunswick, Canada.

Hooge, P. N. and B. Eichenlaub. 2000. Animal movement extension for ArcView. Version 2.0. USDI, Geological Survey, Alaska Science Center, Biological Science Office, Anchorage, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Joseph, V., A. Locke, and J.-G. J. Godin. 2006. Spatial distribution of fishes and decapods in eelgrass (*Zoster marina* L.) and sandy habitats of a New Brunswick estuary, eastern Canada. Aquatic Ecology 40:111–123.

Kahlert, J. 1993. Breeding biology of the Red-breasted Merganser (*Mergus serrator*). Thesis. University of Århus, Århus, Denmark.

Kaminski, R. M. and M. W. Weller. 1992. Breeding habitats of Nearctic waterfowl. Pages 568–589 *in* Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Editors). University of Minnesota Press, Minneapolis, USA.

Klassen, G. J. 2001. Fish and fisheries of Kouchibouguac National Park. Unpublished Report. Memramcook, New Brunswick, Canada.

Korschgen, C. E., K. P. Kenow, W. L. Green, M. D. Samuel, and L. Sileo. 1996. Technique for implanting radio transmitters in day-old ducklings. Journal of Field Ornithology 67:392–397.

Krapu, G. L., P. J. Pietz, D. A. Brandt, and R. R. Cox. 2006. Mallard brood movements, wetland use, and duckling survival during and following a prairie drought. Journal of Wildlife Management 70:1436–1444.

Mauser, D. M., R. L. Jarvis, and D. S. Gilmer. 1994. Movements and habitat use of Mallard broods in northeastern California. Journal of Wildlife Management 58:88–94.

Minot, E. O. 1980. Tidal, diurnal and habitat influences on Common Eider rearing activities. Ornis Scandinavica 11:165–172.

Munro, J. and J. Bédard. 1977. Crèche formation in the Common Eider. Auk 94:759–771.

Palmer, R. S. 1976. Handbook of North American birds. Volume 3. Yale University Press, New Haven, Connecticut, USA.

Pendleton, G. W., K. Titus, E. DeGayner, C. J. Flatten, and R. E. Lowell. 1998. Compositional analysis and GIS for study of habitat selection by goshawks in southeast Alaska. Journal of Agricultural, Biological, and Environmental Statistics 3:280–295.

Pöysä, H. and J. Virtanen. 1994. Habitat selection

and survival of Common Goldeneye (*Bucephala clangula*) broods - preliminary results. Hydrobiologia 279/280:289–296.

RÅD, O. 1980. Breeding distribution and habitat selection of Red-breasted Mergansers in freshwater in western Norway. Wildfowl 31:53–56.

ROTELLA, J. J. AND J. T. RATTI. 1992. Mallard brood movements and wetland selection in southwestern Manitoba. Journal of Wildlife Management 56: 508–515.

SAYLER, R. D. AND M. A. WILLMS. 1997. Brood ecology of Mallards and Gadwalls nesting on islands in large reservoirs. Journal of Wildlife Management 61:808–815.

SJÖBERG, K. 1989. Time-related predator/prey interactions between birds and fish in a northern Swedish river. Oecologia 80:1–10.

SMITH, P. G. 2003. Compos analysis. Version 5.1 standard. Smith Ecology Ltd., Abergavenny, United Kingdom.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry. Second Edition. W.H. Freeman and Company, San Francisco, California, USA.

TALENT, L. G., G. L. KRAPU, AND R. L. JARVIS. 1982. Habitat use by Mallard broods in south central North Dakota. Journal of Wildlife Management 46:629–635.

THOMAS, D. L. AND E. J. TAYLOR. 2006. Study designs and tests of comparing resource use and availability. II. Journal of Wildlife Management 70: 324–336.

TITMAN, R. D. 1999. Red-breasted Merganser (*Mergus serrator*). The birds of North America. Number 443.

WELLER, M. W. 1957. An automatic nest-trap for waterfowl. Journal of Wildlife Management 21:456–458.

WESTERSKOV, K. 1950. Methods for determining the age of game bird eggs. Journal of Wildlife Management 14:56–67.

WHITE, G. C. AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

WHITE, H. C. 1957. Food and natural history of mergansers on salmon waters in the Maritime Provinces of Canada. Fisheries Research Board of Canada Bulletin. Number 116.

WOOD, C. C. 1985. Food-searching behaviour of the Common Merganser (*Mergus merganser*). II. Choice of foraging location. Canadian Journal of Zoology 63:1271–1279.

WOOD, C. C. 1986. Dispersion of Common Merganser (*Mergus merganser*) breeding pairs in relation to the availability of juvenile Pacific salmon in Vancouver Island streams. Canadian Journal of Zoology 64:756–765.

WOOD, C. C. AND C. M. HAND. 1985. Food-searching behaviour of the Common Merganser (*Mergus merganser*) I. Functional responses to prey and predator density. Canadian Journal of Zoology 63: 1260–1270.

YERKES, T. 2000a. Influence of female age and body mass on brood and duckling survival, number of surviving ducklings, and brood movements in Redheads. Condor 102:926–929.

YERKES, T. 2000b. Nest-site characteristics and brood-habitat selection of Redheads: an association between wetland characteristics and success. Wetlands 20:575–580.

YOUNG, A. D. AND R. D. TITMAN. 1986. Costs and benefits to Red-breasted Mergansers nesting in tern and gull colonies. Canadian Journal of Zoology 64:2339–2343.

The Wilson Journal of Ornithology 120(4):755–766, 2008

DIFFERENCES IN GROWTH OF BLACK BRANT GOSLINGS BETWEEN A MAJOR BREEDING COLONY AND OUTLYING BREEDING AGGREGATIONS

CHRISTOPHER A. NICOLAI,[1,3,4] JAMES S. SEDINGER,[1,3] AND MICHAEL L. WEGE[2]

ABSTRACT.—We compared growth rates of Black Brant (*Branta bernicla nigricans*) goslings from two dispersed nesting aggregations to those from the large Tutakoke River Colony on the Yukon-Kuskokwim Delta, Alaska during summers, 1999 and 2000. Approximately 20% of the Black Brant population on the Yukon-Kuskokwim Delta, Alaska nests outside of the four major colonies. Dispersal to these outlying breeding locations is hypothesized as a mechanism by which individuals reduce the negative effects of density dependence associated with major colonies. Growth rates of goslings varied among brood rearing areas both associated with dispersed nesting aggregations (n = 4) and associated with the Tutakoke River Colony (n = 7). Mean mass of goslings, adjusted for age, from brood rearing areas associated with dispersed nesting aggregations ranked sixth, eighth, and ninth of nine brood rearing areas sampled in 1999, and sixth and ninth of nine brood rearing areas sampled in 2000. Mean age-adjusted mass of goslings with the largest mass were 198 and 139 g lighter, respectively, from brood rearing areas associated with a dispersed nesting aggregation than those from brood rearing areas associated with the Tutakoke River colony in 1999 and 2000. Our findings suggest that goslings from dispersed nesting aggregations we sampled are unlikely to have an advantage over goslings from a major colony with respect to survival, adult body size, and recruitment. *Received 7 June 2007. Accepted 9 February 2008.*

Gosling growth rate is highly variable (Cooch et al. 1991, Sedinger and Flint 1991, Aubin et al. 1993) and is governed by both quality and quantity of forage plants (Larsson and Forslund 1991, Cooch et al. 1993, Loonen et al. 1997, Person et al. 2003, Sedinger et al. 2001). Growth rates of goslings have been related to availability of high quality foods at different temporal and spatial scales: (1) among brood-rearing areas associated with a colony (Cooch et al. 1993, Herzog 2002), (2) among colonies (Aubin et al. 1993, Sedinger at al. 2001), (3) among years (Cooch et al. 1991, Sedinger et al. 1998, Person et al. 2003), and (4) among hatch dates (Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994). Food quality (measured as % nitrogen) generally is inversely correlated with plant biomass; when biomass is greater, percent nitrogen content is lower (Sedinger and Raveling 1986, Person et al. 1998, Sedinger et al. 2001). Growth rates of goslings in one study where both quantity and quality were measured (Sedinger et al. 2001) were positively associated with quantity but not quality of grazed vegetation. Strong preference for plant foods with the highest nitrogen content within brood rearing areas, despite substantial biomass of alternative plant foods of lower nitrogen content (Harwood 1977, Sedinger and Raveling 1984), indicates that plant foods below some minimum level of nitrogen concentration will not sustain high rates of growth in goslings.

Density of broods is often negatively correlated with availability of high quality foods (Cooch et al. 1993; Person et al. 1998; Sedinger et al. 1998, 2001) and growth rates of goslings are negatively correlated with local population density (Cooch et al. 1991, Person et al. 2003). Reduced gosling growth at higher population densities is a principal mechanism regulating local breeding populations of geese because first-year survival is highly correlated with gosling body size late in their first summer (Francis and Cooke 1992, Schmutz 1993, Sedinger and Chelgren 2007). Growth rate may also affect adult body size (Cooch et al.

[1] Department of Biology and Wildlife and Institute of Arctic Biology, University of Alaska Fairbanks, 211 Irving I, Fairbanks, AK 99775, USA.

[2] U.S. Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, P. O. Box 346, Bethel, AK 99559, USA.

[3] Current address: Department of Natural Resources and Environmental Science, University of Nevada Reno, 1000 Valley Road, Reno, NV 89512, USA.

[4] Corresponding author; e-mail: nicolai@unr.nevada.edu

1991, Larson and Forslund 1991, Sedinger et al. 1995) and future fecundity (Sedinger et al. 1995). Density-dependent regulation of populations of arctic nesting geese is largely mediated through increased competition for sufficiently high quality food for growing goslings (Cooch et al. 1993, Black et al. 1998, Sedinger et al. 2001). Thus, understanding how individuals respond to local density or population size is important.

Density-dependent effects could be reduced by (1) parents from a particular nesting area dispersing with broods to brood-rearing areas of lower density (e.g., Cooch et al. 1993, Slattery 2000, Mainguy et al. 2006), or (2) natal or breeding dispersal to new nesting areas away from major colonies (e.g., Black et al. 1998) and using brood-rearing areas associated with these dispersed breeding locations. Either mechanism could expose goslings to improved foraging conditions and potentially result in increased recruitment and future fecundity (Black et al. 2007).

Approximately 75% of the breeding Black Brant (*Branta bernicla nigricans*; hereafter Brant) population nests on the Yukon-Kuskokwim (Y-K) Delta (Sedinger et al. 1993). Most (80%) Brant on the Y-K Delta nest in four major colonies and the remainder nest in small aggregations (Sedinger et al. 1993), which we define as dispersed nesting aggregations. Numbers of nests in the four major colonies increased from 12,000 to >25,000 between 1982 and 2000 (Sedinger et al. 1993; Anthony et al. 1995; R. M. Anthony, USGS, unpubl. report Anchorage, AK), although numbers in major colonies are generally below historic levels. Numbers of nests in dispersed aggregations range from <10 nests to several hundred nests and Brant may also nest solitarily. Local density, through its impact on food abundance (Person et al. 1998), has reduced gosling growth rates at the two largest colonies on the Y-K Delta (Sedinger et al. 1998, 2001). Concurrently, numbers of Brant nesting in dispersed nesting aggregations have increased (Robert Stehn, U.S. Fish and Wildlife Service, unpubl. report). Natal philopatry by females to main colonies is high (0.83) but not absolute for female Brant (Lindberg et al. 1998, Sedinger et al. 2008), suggesting that dispersal from major colonies could contribute to growth of dispersed nesting aggregations. We did encounter individual female Brant ($n < 100$) originally marked in major colonies nesting in dispersed nesting aggregations (pers. obs.). Yet, if goslings produced in dispersed nesting aggregations grew sufficiently rapidly, recruitment by these goslings would also provide a mechanism explaining growth of satellite breeding aggregations.

Our objective was to compare growth rates of Brant goslings from a major colony (Tutakoke River) with those from two dispersed nesting aggregations to test the hypothesis that individuals hatched outside the largest colonies experienced improved foraging conditions relative to those from the main colonies. We include measures of culmen and tarsus growth as these skeletal measures tend to be more conserved when nutrients are limiting (Sedinger et al. 2001). Responses of these two measures provide a stronger indication of growth responses to variation in nutrient availability among brood rearing areas than does mass (Cooch et al. 1991). We address the potential benefits to gosling growth that would result from immigrating to dispersed nesting aggregations. Our study differs from that of Cooch et al. (1993) who studied benefits of moving to new brood-rearing areas by Lesser Snow Geese (*Chen caerulescens caerulescens*) that had not changed nesting location.

METHODS

Field Methods.—We monitored goslings originating from one large colony (Tutakoke River Colony; hereafter TRC) and two dispersed nesting aggregations (Big Slough and Aknerkochik River) on the outer coastal fringe in the central part of the Y-K Delta in western Alaska (Fig. 1). The Big Slough dispersed nesting aggregation had 347 nests in 1992 (M. S. Lindberg, pers. comm.). This number increased to 749 nests in 1999 (Nicolai 2003).

Color banding has been conducted at TRC since 1984. All nests in which at least one parent was marked were visited at least every other day after hatch began at TRC. All nests at Big Slough and Aknerkochik River were checked daily for hatching goslings. We applied individually coded, fish-fingerling tags to the foot webbing of hatched goslings and goslings in pipping eggs (Alliston 1975). We were able to assign gosling ages to within ±1

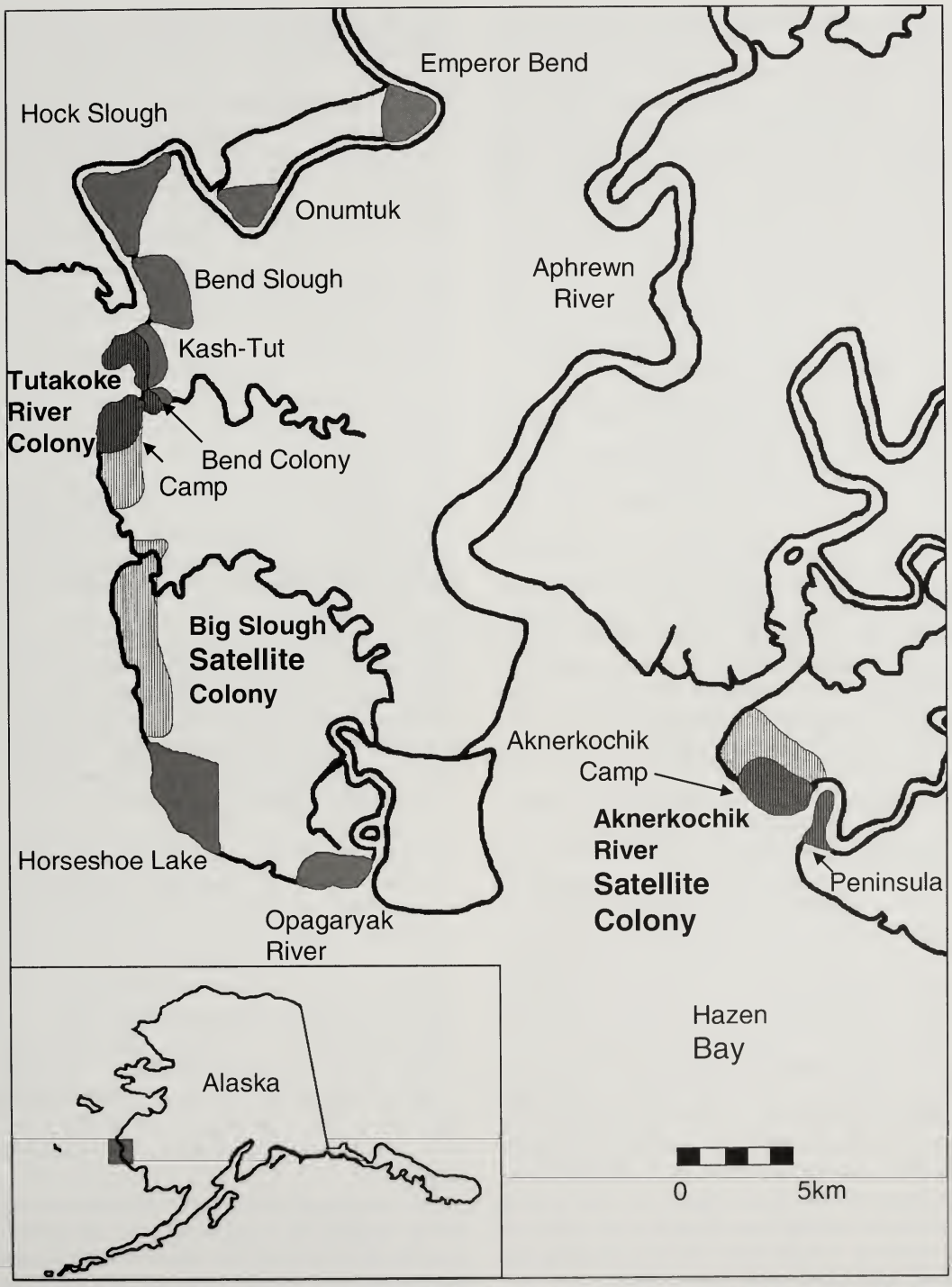


FIG. 1. Study and brood rearing areas on the Yukon-Kuskokwim Delta, Alaska. Shaded areas refer to brood rearing areas. Hatched areas and bold type refer to nesting areas where web-tags were attached.

day because hatching of individual clutches requires ~24 hrs. Following hatch, broods move to rearing areas up to 40 km from nest sites (Lindberg et al. 1997) where they have relatively well defined home ranges (Flint and Sedinger 1992). Tracking radio-tagged adult females at hatch in 1999 indicated that most broods at Big Slough moved to one general brood rearing area (Horseshoe Lake), whereas broods from Aknerkochik River displayed a more widespread movement of broods (unpubl. data). We recaptured goslings in corral traps during adult remigial molt (Sedinger et al. 1997: Fig. 1). We captured goslings over a range of ages (16–36 days of age) when growth was approximately linear. We weighed goslings using spring scales (±5 g) and measured diagonal tarsus, and total culmen using dial calipers (±0.1 mm; Dzubin and Cooch 1992).

Statistical Analysis.—Actual density of broods on brood-rearing areas is rarely measured because of logistical difficulties associated with estimates for mobile species (but see Herzog 2002). Rather, size of goslings near fledging, which is affected by their rate of growth, is used as a surrogate for density of broods relative to availability of sufficiently high quality food (e.g., Cooch et al. 1993). We used the same approach because the key question was, can individuals improve foraging conditions and fitness for their goslings by moving to dispersed nesting aggregations, where competition for food might be reduced?

We used the mixed model procedure in SAS (SAS Institute 1989) to assess variation in gosling measurements among brood rearing areas. We included year, gender, and brood rearing area as fixed effects and age as a covariate. We included brood identity as a random variable in the analysis to control for within-brood effects. This model structure treated individual broods (not individual goslings) as the independent sampling unit for assessment of the fixed effects of year, gender, and brood rearing area. Brood mates were not considered independent when evaluating variation associated with fixed effects.

We did not include hatch dates in the analyses for three reasons. First, hatch date relative to other goslings using the same brood-rearing area (rather than absolute hatch date) was likely the component of hatch date most relevant to within brood rearing area variation in growth (Cooch et al. 1991, Sedinger and Flint 1991, Sedinger et al. 1997). Failure to account for relative hatch dates increased the within-brood rearing area residual variance, rendering our analysis more conservative, unless there was substantial intermixing of goslings from two colonies with substantially different mean hatch dates. Second, if differences in hatch date between major colonies and dispersed nesting aggregations created an advantage for goslings from major colonies, this advantage would be one mechanism nullifying the benefit of dispersal. Third, and most important, both application of web-tags and recapture of web-tagged gosling occur over relatively short periods within years and colonies: ~10 days for application of web-tags and 4 days for recapture. Models containing a brood-rearing area*year interaction created nearly complete confounding between gosling age and hatch date because each brood-rearing area was sampled on only 1 day each year (Herzog 2002). The single annual sample from each brood-rearing area, combined with the negative covariance between gosling age and hatch date and the narrow range of gosling ages and hatch dates, made it virtually impossible to simultaneously estimate the effects of both gosling age and hatch date in models.

Candidate models included all possible combinations of year, gender, brood-rearing area and age, including all two-way interactions. We used a maximum likelihood approach to generate parameter estimates and the Satterthwaite method (Kuehl 2000) to calculate denominator degrees of freedom. We used an information theoretic approach based on Aikaike's Information Criterion adjusted for small sample size (AIC*c*) (Burnham and Anderson 1998, Anderson et al. 2000) to assess hypotheses represented by candidate models.

We examined sources of variation in selected models by using estimates of covariance from results of the mixed model to estimate variation within random variables. Covariance parameters estimated the variance associated with random effects within residual error. We analyzed the same data set using a general linear model (SAS Institute 1989) and estimated variance for fixed effects and error.

TABLE 1. Number of web-tagged goslings and broods captured in banding drives. Two areas were sampled in each of the two dispersed nesting aggregations and seven areas were sampled associated with the Tutakoke River Colony. Brood rearing areas not sampled are designated N/S.

Nesting area/ Brood area	1999		2000	
	Goslings	Broods	Goslings	Broods
Aknerkochik River				
Camp	8	5	N/S	N/S
Peninsula	3	2	N/S	N/S
Big Slough				
Horseshoe Lake	53	33	14	12
Opagaryak River	N/S	N/S	13	11
Tutakoke River				
Camp	38	24	13	9
Bend Colony	10	5	3	3
Kash-Tut	124	72	40	27
Bend Slough	138	91	42	30
Hock Slough	107	64	80	60
Onumtuk	6	5	2	2
Emperor Bend	0	0	5	4

We allowed sums of the covariance parameter estimates from the mixed model to equal error sums of squares from the linear model while maintaining the proportions of the covariance parameter estimates. We present variance components from mixed model analysis of variance to allow an assessment of the contributions of variables to the overall variance in the dependant variable. Hypothesis tests were not consistent with the information theoretic approaches we used to assess models and we did not use variance components to test hypotheses in the traditional sense. We present least square means ± SE for mass, culmen, and tarsus. We used model-averaged parameter estimates to depict variation in mass, culmen, and tarsus with respect to age, year, and brood-rearing area.

RESULTS

We recaptured 487 and 212 web-tagged goslings from 301 and 158 broods in 1999 and 2000, respectively (Table 1.). Tracking radio-tagged adult females at hatch in 1999 indicated that most broods at Big Slough moved to one general brood rearing area (Horseshoe Lake), whereas broods from Aknerkochik River displayed a more widespread movement. We captured goslings on two brood rearing areas associated with the Aknerkochik River dispersed nesting aggregation, two areas associated with the Big Slough dispersed nesting aggregation, and seven areas associated with TRC. Twelve goslings from TRC were recaptured at brood rearing areas principally associated with Big Slough and six goslings from Big Slough were recaptured at brood rearing areas associated with TRC, which represented 2 and 8%, respectively, of goslings captured from the two breeding locations. Broods associated with specific brood rearing areas were primarily associated with the breeding locations we assumed in our analyses. Mean hatch dates for captured web-tagged goslings among breeding colonies (including TRC and both dispersed nesting aggregations) and years varied by less than 0.5 days. Modal hatch dates were similar in 2000 among breeding colonies; however modal hatch dates varied slightly in 1999: Julian date 176 for Aknerkochik River, Julian date 177 for Big Slough, and Julian date 173 for Tutakoke River. Mean hatch dates of recaptured goslings followed a similar pattern to modal hatch dates among breeding colonies (mean difference 0 days), indicating that hatch dates of our samples relative to their colony means were similar among our samples from different breeding locations.

Eight models for gosling mass were within four $\Delta AICc$ units of each other (Table 2). These eight models contained effects of brood rearing area, year, gender, age, and brood, but had different combinations of interactions. All competing models of mass contained the effects of brood-rearing area, gender, and age, and a year*brood-rearing area interaction (Table 2). Mass of goslings, after adjusting for age, from brood-rearing areas associated with dispersed breeding aggregations, ranked sixth, eighth, and ninth of nine areas in 1999, and sixth and ninth of nine areas sampled in 2000 (Table 3, Fig. 2). Age-adjusted masses for goslings from the dispersed breeding aggregation with the largest size were 198 and 139 g smaller than those from TRC brood rearing areas which produced the largest goslings in 1999 and 2000, respectively. Goslings from brood-rearing areas associated with dispersed breeding aggregations were 28 and 44 g smaller than goslings from TRC brood rearing areas producing the smallest goslings in 1999 and 2000, respectively (Fig. 2).

TABLE 2. AIC*c* model selection for gosling mass. All models with ΔAIC*c* ≤4.0 and the general model are presented.

Model[a]	np[b]	AIC*c*	ΔAIC*c*	Model weight
Y S BRA A Y*S Y*BRA S*A B	24	7911.5	0.0	0.2047
Y S BRA A Y*BRA S*A B	23	7911.6	0.1	0.1947
Y S BRA A Y*BRA B	22	7912.0	0.5	0.1594
Y S BRA A Y*S Y*A Y*BRA S*A B	25	7912.9	1.4	0.1017
Y S BRA A Y*A Y*BRA S*A B	24	7913.0	1.5	0.0967
Y S BRA A Y*A Y*BRA B	23	7913.4	1.9	0.0792
Y S BRA A Y*S Y*BRA B	23	7914.0	2.5	0.0587
Y S BRA A Y*S Y*A Y*BRA B	24	7915.5	4.0	0.0277
Y S BRA A Y*S Y*BRA Y*A S*BRA S*A BRA*AGE B	43	7934.9	23.4	0.0000

[a] Y = Year, S = Gender, BRA = Brood Rearing Area, A = Age, and B = Brood.
[b] np = Number of parameters in model.

Model selection for tarsus length resulted in four models with ΔAIC*c* ≤ 4.0, all contained variation among brood-rearing area, years, genders, and ages with different combinations of two-way interactions (Table 4). Tarsus length of goslings from dispersed breeding aggregations, after adjusting for age, ranked sixth, eighth, and ninth in 1999, and eight and ninth in 2000 (Table 3, Fig. 3). Seven models for gosling culmen length had ΔAIC*c* ≤ 4.0 and all models contained brood-rearing area, years, gender, and age except for the seventh ranked model (ΔAIC*c* = 2.6) which did not contain a gender effect (Table 5). Age-adjusted estimates of culmen length for goslings from dispersed breeding aggregations ranked fourth, sixth, and ninth in 1999 and seventh and ninth in 2000 (Table 3, Fig. 4).

Males weighed 31.6 ± 5.6 g more than females after adjusting for age and had tarsi and culmens that were 2.3 ± 0.3 mm and 0.21 ± 0.12 mm longer than those of females, respectively (Figs. 2–4). Goslings of the same age weighed 298.9 ± 64.8 g more and had tarsi and culmens that were 6.2 ± 3.8 mm and 2.3 ± 1.6 mm longer in 1999 than in 2000, respectively (Figs. 2–4). We estimated that gosling age accounted for 36% of the variance in gosling mass, followed by the random effect brood (16% of variance), year (13.5%) and brood-rearing area (9%) (Table 6). Variables we considered explained 77% of the variance in gosling mass.

DISCUSSION

Gosling growth varied among brood rearing areas both within and among areas primarily associated with TRC and two dispersed nesting aggregations. Variation in gosling growth among brood rearing areas also occurs in other goose populations (Larsson and Forslund 1991, Aubin et al. 1993, Sedinger et al. 2001) and has been related to availability and quality of forage (Cooch et al. 1991, Sedinger and Flint 1991, Manseau and Gauthier 1993). Person et al. (1998) found forage quantity varied substantially among brood rearing areas associated with the TRC. Areas with the highest forage quantity (Person et al. 1998) supported the largest goslings in the current study.

Gosling size on brood rearing areas associated with dispersed nesting aggregations was smaller than or similar to that of goslings from TRC. These findings indicate that goslings produced in dispersed nesting aggregations at the time of this study did not experience reduced competition for food, as indicated by growth rates. Sedinger et al. (2001) showed that Brant goslings from the Colville River Delta (70° N 149° W) on Alaska's arctic coast were ~300 g larger (adjusted for age) than goslings from TRC and the Kochechik Bay colony (62° N 166° W), another major colony on the Y-K Delta. These results indicate that growth rate of goslings at dispersed nesting aggregations on the Y-K Delta is below the maximum possible, which is also the case at the major colonies on the Y-K Delta.

Gosling growth directly affects first-year survival and consequently recruitment into the breeding population (Owen and Black 1989, Cooch et al. 1991, Sedinger et al. 1995). Our findings suggest that recruitment rates are unlikely to be greater for goslings from dis-

TABLE 3. Rankings of brood rearing areas by measurement and year based on Least Squares Means. Lowest values indicate largest size among brood rearing areas within measurement and year. Brood rearing areas not sampled or for which no web-tagged goslings were captured are denoted N/S.

Colony/ Brood rearing area	Mass		Tarsus		Culmen	
	1999	2000	1999	2000	1999	2000
Aknerkochik River						
Camp	8	N/S	8	N/S	6	N/S
Peninsula	6	N/S	6	N/S	4	N/S
Big Slough						
Horseshoe Lake	9	9	9	9	9	7
Opagaryak River	N/S	6	N/S	8	N/S	9
Tutakoke River						
Camp	4	8	4	6	7	5
Bend Colony	5	3	5	7	1	6
Kash-Tut	7	7	7	4	8	8
Bend Slough	3	5	3	5	5	3
Hock Slough	2	4	2	3	3	1
Onumtuk	1	2	1	2	2	2
Emperor Bend	N/S	1	N/S	1	N/S	4

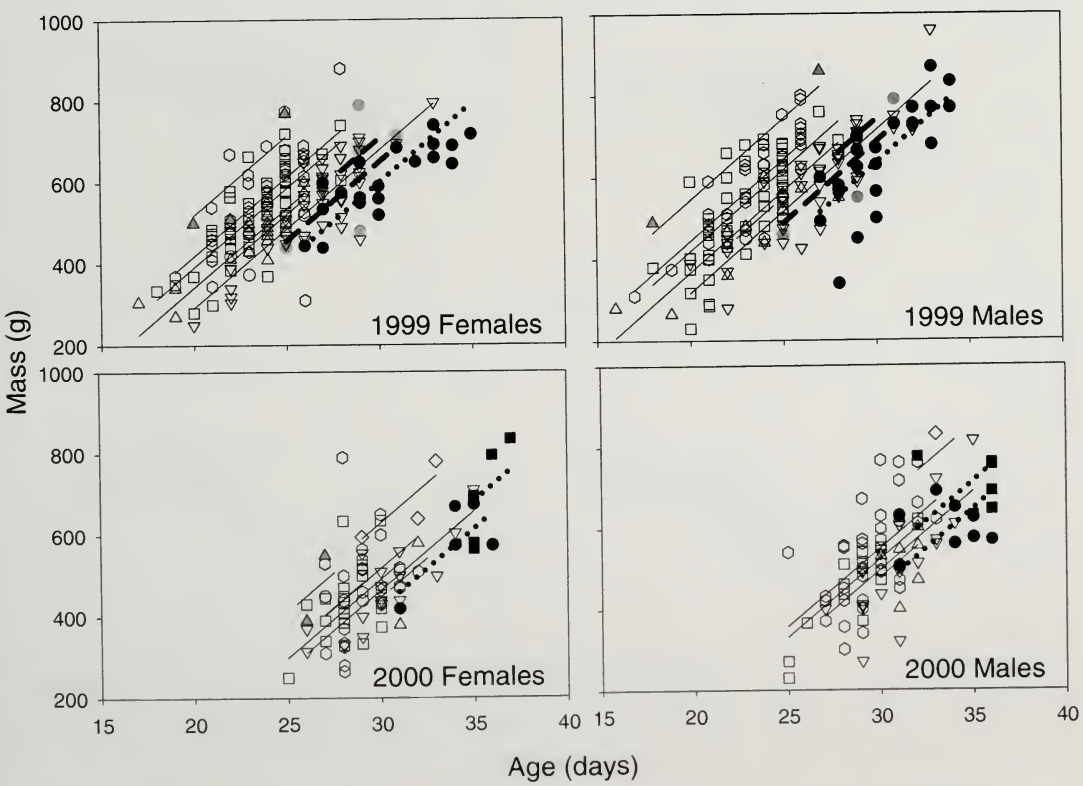


FIG. 2. Model averaged Least Squares Means for gosling mass (g) vs. age (days). Filled symbols and heavy lines represent brood rearing areas for dispersed nesting aggregations. Open symbols and thin lines represent brood rearing areas from the Tutakoke River Colony. Only individual broods are presented as symbols. Gosling mass was averaged among brood mates within the same year and gender.

TABLE 4. AIC*c* model selection for gosling tarsus length. All models with ΔAIC*c* ≤4.0 and the general model are presented.

Model[a]	np[b]	AIC*c*	ΔAIC*c*	Model weight
Y S BRA A Y*BRA A*BRA B	30	3810.1	0.0	0.3844
Y S BRA A Y*BRA S*A A*BRA B	31	3812.2	2.1	0.1345
Y S BRA A Y*A Y*BRA A*BRA B	31	3812.2	2.1	0.1345
Y S BRA A Y*S Y*BRA A*BRA B	31	3812.2	2.1	0.1345
Y S BRA A Y*S Y*BRA Y*A S*BRA S*A BRA*AGE B	43	3832.1	22.0	0.0000

[a] Y = Year, S = Gender, BRA = Brood Rearing Area, A = Age, and B = Brood.
[b] np = Number of parameters in model.

persed nesting aggregations compared to those from major colonies. Additionally, nest success is typically lower in dispersed breeding aggregations than major colonies (0.2–0.5 vs. 0.7–0.8) (Raveling 1989; J. S. Sedinger, unpubl. data), which was also true during our study. Nest success in the dispersed nesting aggregations averaged 65% between 1998 and 2000 compared to 80% in the TRC (unpubl. data). We suggest that natal or breeding dispersal from major colonies on the Y-K Delta to dispersed nesting areas would not improve foraging conditions experienced by goslings during the growth period. The hypothesis that dispersers reduce the influence of local density dependence during brood rearing depends

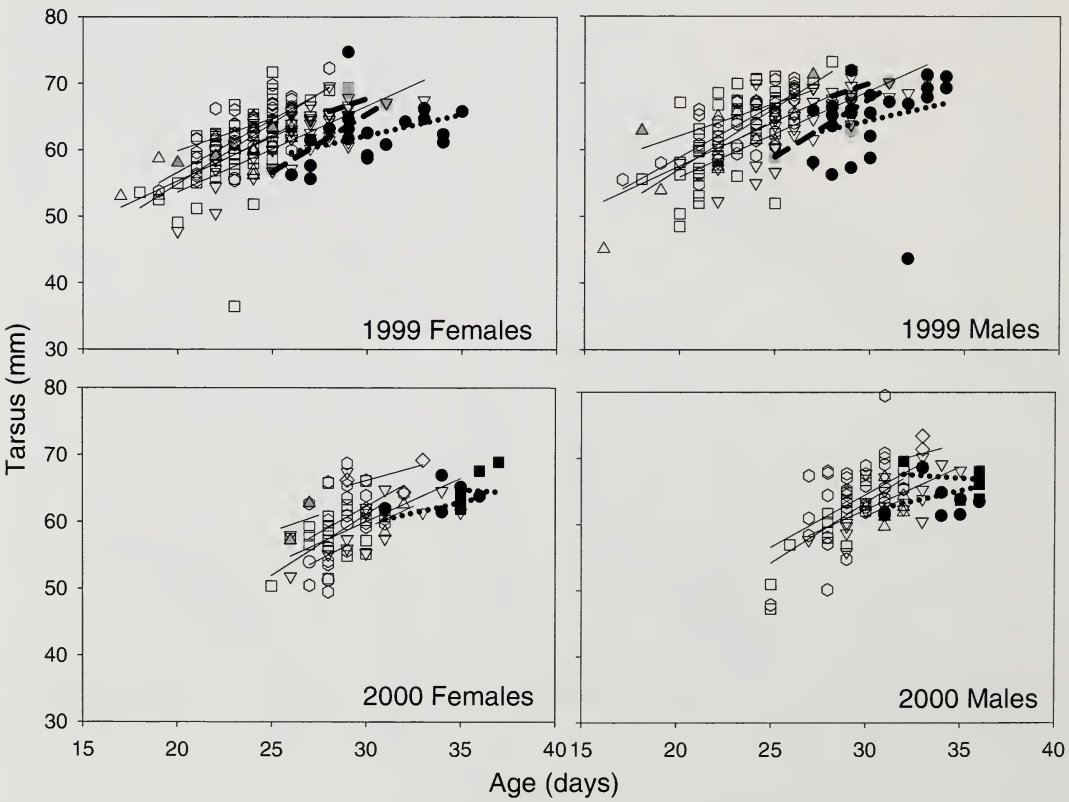


FIG. 3. Model averaged Least Squares Means for gosling tarsal length (mm) vs. age (days). Filled symbols and heavy lines represent brood rearing areas for dispersed nesting aggregations. Open symbols and thin lines represent brood rearing areas from the Tutakoke River Colony. Only individual broods are presented as symbols. Gosling tarsal length was averaged among brood mates within the same year and gender.

TABLE 5. AIC*c* model selection for gosling culmen length. All models with ΔAIC*c* ≤4.0 and the general model are presented.

Model[a]	np[b]	AIC*c*	ΔAIC*c*	Model weight
Y S BRA A Y*BRA A*BRA B	30	2644.1	0.0	0.2710
Y BRA A Y*BRA S*A A*BRA B	31	2644.6	0.5	0.2110
Y S BRA A Y*A Y*BRA A*BRA B	31	2646.0	1.9	0.1048
Y S BRA A Y*S Y*BRA S*A A*BRA B	32	2646.3	2.2	0.0902
Y S BRA A Y*S Y*BRA A*BRA B	31	2646.3	2.2	0.0902
Y S BRA A Y*A Y*BRA S*A A*BRA B	32	2646.6	2.5	0.0776
Y BRA A Y*A Y*BRA A*BRA B	30	2646.7	2.6	0.0738
Y S BRA A Y*S Y*BRA Y*A S*BRA S*A BRA*AGE B	43	2664.0	19.9	0.0000

[a] Y = Year, S = Gender, BRA = Brood Rearing Area, A = Age, and B = Brood.
[b] np = Number of parameters in model.

on their use of brood rearing areas distinct from those used by broods originating from major colonies. We observed a relatively small amount of mixing on brood rearing areas; ≤8% of goslings from each colony were captured on brood-rearing areas used primarily by broods from the other colony. Even if mixing was substantial, it would be another mechanism reducing the benefits of breeding dispersal.

We cannot assess the most interesting hypothesis: what would have been the fates of the young of dispersing individuals had they not dispersed? It is possible dispersing indi-

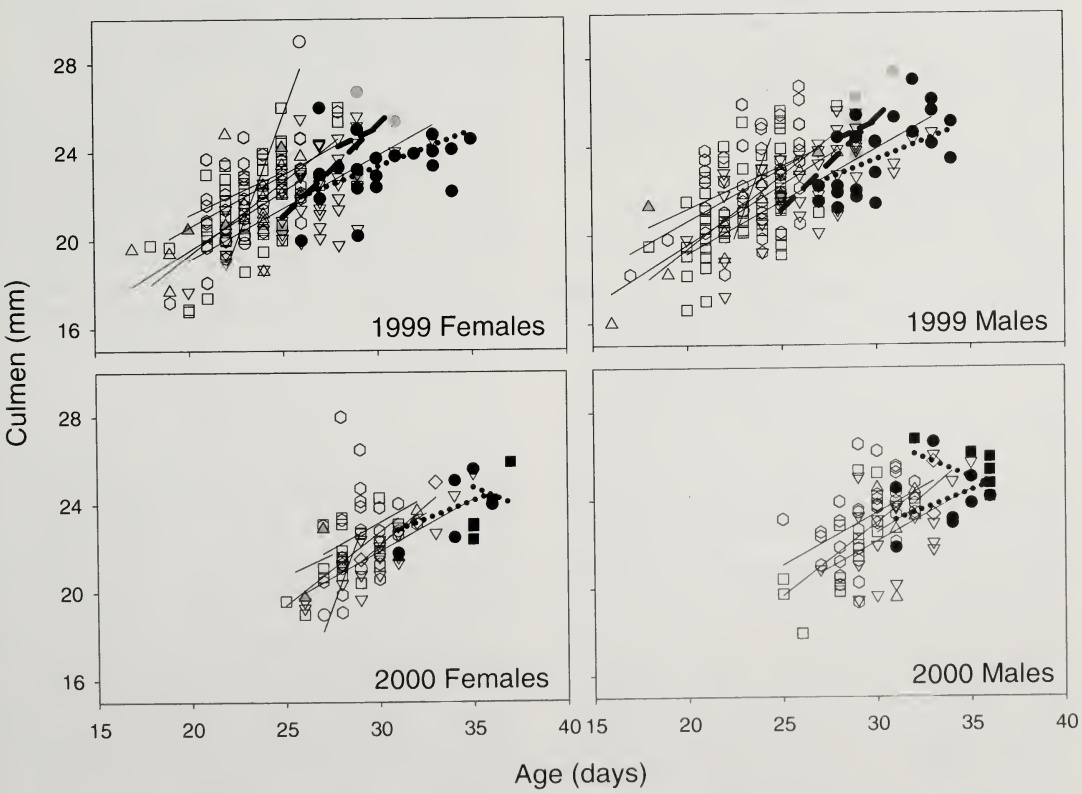


FIG. 4. Model averaged Least Squares Means for gosling culmen length (mm) vs. age (days). Filled symbols and heavy lines represent brood rearing areas for dispersed nesting aggregations. Open symbols and thin lines represent brood rearing areas from the Tutakoke River Colony. Only individual broods are presented as symbols. Gosling culmen length was averaged among brood mates within year and gender.

TABLE 6. Mixed model variance partitioning for three measurements of growth. Values are percentages of total variance within each measurement.

Effect	Measurement		
	Mass	Culmen	Tarsus
Year	13.5	11.2	11.8
Gender	1.3	0.5	11.0
Age	36.1	11.7	7.0
Brood Rearing Area	9.1	7.2	4.6
Year × Brood Rearing Area	1.4	5.5	6.4
Age × Brood Rearing Area		7.4	5.6
Brood	16.0	9.4	20.8
Residual	22.7	47.1	32.8

viduals achieved some benefit by dispersing, relative to not doing so. It is also possible that, overall, the population recruited more young than would have occurred without dispersal, because individuals within the population showed a combination of fidelity to major colonies and dispersal to dispersed breeding aggregations. For Lesser Snow Geese, however, dispersal provides an absolute benefit: growth rates are higher for individuals that dispersed than for those that did not (Cooch et al. 1993). A reasonable question, therefore, is whether such a pattern exists for Brant?

We could not assess parental quality for goslings originating from dispersed nesting aggregations because most adults from these aggregations were unmarked. Thus, we could not evaluate the potential that lower quality parents nested in dispersed nesting aggregations, resulting in slower growth of their goslings relative to those from major colonies. Lindberg et al. (1998) showed natal and adult dispersal from TRC, and we encountered marked adults originally marked in areas not associated with these dispersed nesting aggregations. Effects of parental quality on gosling growth are typically believed to involve social interactions between broods and variation in dominance (Williams et al. 1994, Loonen et al. 1997, Black et al. 2007). Thus, quality of parents relative to each other, not absolute quality, influences growth rate of goslings. Even if parents from dispersed nesting aggregations were of lower quality than those from the major colony, we would not expect reduced growth rates of goslings from dispersed nesting aggregations as long as they were not competing primarily with broods from the major colony, for which we found no evidence.

Dispersal from major colonies to dispersed nesting aggregations occurs, but goslings of emigrants apparently do not benefit from reduced density dependence mediated through reduced competition for food. Masses of goslings from dispersed nesting aggregations would have reduced first-year survival by about 20%, relative to those from TRC (Sedinger and Chelgren 2007). Modeling of the Y-K Delta Brant population (J. S. Sedinger and N. D. Chelgren, unpubl. report) indicates that low nest success of Brant in dispersed nesting aggregations is sufficient to reduce λ (per capita rate of increase) in these areas to <1. Goslings from dispersed nesting aggregations were relatively small with low first-year survival; our data suggest that recent increases in numbers of Brant nesting in dispersed nesting aggregations must result at least partially from immigration from major colonies. We suggest the hypothesis that dispersed nesting aggregations may not be sustained by *in situ* recruitment; rather, they are likely augmented by immigration from major colonies. Dispersed nesting aggregations may provide some release for major colonies when nesting densities become high, producing higher fitness for individual breeders than they would have experienced had they not dispersed, and a greater overall rate of population increase than would have occurred in the absence of dispersal.

ACKNOWLEDGMENTS

The U.S. Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, U.S. Park Service, National Science Foundation (OPP-9985931), Ducks Unlimited Inc., and the University of Alaska Fairbanks provided funding for this project. J. P. Arturo, M. R. Axelson, T. W. Bentsen, L. M Bernstein, C. J. Brown, B. C. Comstock, T. R. Dixon, T. R. Jones, B. A. Lorenz, R. L. McQuire, William Naneng, K. L. Nicholson, A. J. Nicolai, T. J. Olson, B. T. Person, D. R. Ruthrauff, M. B. Sato, J. L. Schamber, and C. R. Villa provided field assistance. Logistical support was provided by Yukon Delta National Wildlife Refuge. M. P. Herzog provided unpublished data and invaluable suggestions for statistical analysis. Graduate committee members, R. W. Ruess and P. S. Barboza provided valuable insight throughout this project. P. L. Flint, R. F. Rockwell, and J. A. Schmutz commented on an earlier draft of the manuscript.

LITERATURE CITED

Alliston, W. G. 1975. Web tagging ducklings in pipped eggs. Journal of Wildlife Management 39: 625–628.

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912–923.

Anthony, R. M., W. H. Anderson, J. S. Sedinger, and L. L. McDonald. 1995. Estimating populations of nesting Brant using aerial videography. Wildlife Society Bulletin 23:80–87.

Aubin, A. E., A. Dzubin, E. H. Dunn, and C. D. MacInnes. 1993. Effects of summer feeding area on gosling growth in Snow Geese. Ornis Scandinavica 24:255–260.

Black, J. M., J. Prop, and K. Larsson. 2007. Wild goose dilemmas. Branta Press, Groningen, The Netherlands.

Black, J. M., E. G. Cooch, M. J. J. E. Loonen, R. H. Drent, and M. Owen. 1998. Body size variation in Barnacle Goose colonies: evidence for local saturation of habitats. Norsk Polarinstitutt Skrifter 200:129–140.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York, USA.

Cooch, E. G., R. L. Jeffries, R. F. Rockwell, and F. Cooke. 1993. Environmental change and the cost of philopatry: an example in the Lesser Snow Goose. Oecologia 93:128–138.

Cooch, E. G., D. B. Lank, A. Dzubin, R. F. Rockwell, and F. Cooke. 1991. Body size variation in Lesser Snow Geese: environmental plasticity in gosling growth rates. Ecology 72:503–512.

Dzubin, A. and E. G. Cooch. 1992. Measurements of geese: general field methods. California Waterfowl Association, Sacramento, California, USA.

Flint, P. L. and J. S. Sedinger. 1992. Reproductive implications of egg size in Black Brant. Auk 109: 896–903.

Francis, C. M. and F. Cooke. 1992. Sexual differences in survival and recovery rates of Lesser Snow Geese. Journal of Wildlife Management 56:287–296.

Harwood, J. 1977. Summer feeding ecology of Lesser Snow Geese. Journal of Wildlife Management 41: 48–55.

Herzog, M. P. 2002. Environmental regulation of growth in Black Brant. Dissertation. University of Alaska, Fairbanks, USA.

Kuehl, R. O. 2000. Design of experiments: statistical principles of research design and analysis. Second Edition. Duxbury Press, Pacific Grove, California, USA.

Larsson, K. and P. Forslund. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619–636.

Lindberg, M. S., J. S. Sedinger, and P. L. Flint. 1997. Effect of spring environment and nesting phenology on clutch size in Black Brant. Condor 99: 381–388.

Lindberg, M. S., J. S. Sedinger, D. V. Derksen, and R. F. Rockwell. 1998. Natal and breeding philopatry in a Black Brant, *Branta bernicla nigricans*, metapopulation. Ecology 79:1893–1904.

Lindholm, A., G. Gauthier, and A. Desrochers. 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting Greater Snow Geese. Condor 94:898–908.

Loonen, M. J. J. E., K. Oosterbeek, and R. H. Drent. 1997. Variation in growth of young and adult size in Barnacle Geese *Branta leucopsis*: evidence for density dependence. Ardea 85:177–192.

Mainguy, J., G. Gauthier, J. F. Giroux, and J. Bety. 2006. Gosling growth and survival in relation to brood movements in Greater Snow Geese (*Chen caerulescens atlantica*). Auk 123:1077–1089.

Manseau, M. and G. Gauthier. 1993. Interactions between Greater Snow Geese and their rearing habitat. Ecology 74:2045–2055.

Nicolai, C. A. 2003. Reproductive decisions by Black Brant: mechanisms to synchronize hatch and spatial variation in growth rates of goslings. Thesis. University of Alaska, Fairbanks, USA.

Owen, M. and J. M. Black. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. Journal of Animal Ecology 58:603–617.

Person, B. T., C. A. Babcock, and R. W. Ruess. 1998. Forage variation in brood-rearing areas used by Pacific Black Brant Geese on the Yukon-Kuskokwim Delta, Alaska. Journal of Ecology 86:243–259.

Person, B. T., M. P. Herzog, R. W. Ruess, J. S. Sedinger, R. M. Anthony, and C. A. Babcock. 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia 135:583–592.

Raveling, D. G. 1989. Nest-predation rates in relation to colony size of Black Brant. Journal of Wildlife Management 53:87–90.

SAS Institute. 1989. SAS User's Guide. Version 6. Fourth Edition. SAS Institute Inc., Cary, North Carolina, USA.

Schmutz, J. A. 1993. Survival and pre-fledging body mass in juvenile Emperor Geese. Condor 95:222–225.

Sedinger, J. S. and N. D. Chelgren. 2007. Survival and breeding advantages of larger Black Brant goslings: within and among cohort variation. Auk 124:1281–1293.

Sedinger, J. S. and P. L. Flint. 1991. Growth rate is negatively correlated with hatch date in Black Brant. Ecology 72:496–502.

Sedinger, J. S. and D. G. Raveling. 1984. Dietary selectivity in relation to availability and quality of food for goslings of Cackling Geese. Auk 101: 295–306.

SEDINGER, J. S. AND D. G. RAVELING. 1986. Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. Journal of Animal Ecology 55:1083–1102.

SEDINGER, J. S., P. L. FLINT, AND M. S. LINDBERG. 1995. Environmental influence on life-history traits: growth, survival, and fecundity in Black Brant (*Branta bernicla*). Ecology 76:2404–2414.

SEDINGER, J. S., N. D. CHELGREN, D. H. WARD, AND M. S. LINDBERG. 2008. Fidelity and breeding probability related to population density and individual quality on Black Brant Geese (*Branta bernicla nigricans*). Journal of Animal Ecology 77: In press.

SEDINGER, J. S., M. S. LINDBERG, M. W. EICHHOLZ, AND N. CHELGREN. 1997. Influence of hatch date versus maternal and genetic effects on growth of Black Brant goslings. Auk 114:129–132.

SEDINGER, J. S., C. J. LENSINK, D. H. WARD, R. M. ANTHONY, M. L. WEGE, AND G. V. BYRD. 1993. Status and recent dynamics of the Black Brant breeding population. Wildfowl 44:49–59.

SEDINGER, J. S., M. S. LINDBERG, B. T. PERSON, M. W. EICHHOLZ, M. P. HERZOG, AND P. L. FLINT. 1998. Density-dependent effects on growth, body size, and clutch size in Brant. Auk 115:613–620.

SEDINGER, J. S., M. P. HERZOG, B. T. PERSON, M. T. KIRK, T. OBRITCHKEWITCH, P. P. MARTIN, AND A. A. STICKNEY. 2001. Large-scale variation in growth of Black Brant goslings related to food availability. Auk 118:1088–1095.

SLATTERY, S. M. 2000. Factors affecting first-year survival in Ross' Geese. Dissertation. University of Saskatchewan, Saskatoon, Canada.

WILLIAMS, T. D., M. J. J. E. LOONEN, AND F. COOKE. 1994. Fitness consequences of parental behavior in relation to offspring number in a precocial species - the Lesser Snow Goose. Auk 111:563–572.

The Wilson Journal of Ornithology 120(4):767–777, 2008

DIET OF THE YELLOW-KNOBBED CURASSOW IN THE CENTRAL VENEZUELAN LLANOS

CAROLINA BERTSCH[1,2] AND GUILLERMO R. BARRETO[1]

ABSTRACT.—Curassows (Cracidae) are important components of the avian biomass in neotropical frugivorous bird communities. However, their feeding habits and ecological role remain unclear. We identified the diet of wild Yellow-knobbed Curassow (*Crax daubentoni*) based on analyses of feces and direct observations from November 2001 to July 2002 in a tropical dry forest in central Venezuela. We also analyzed stomach contents from specimens collected in different localities throughout the Llanos region. The diet of curassows included fruits (41 and 49% of dry weight in feces and stomach contents, respectively), seeds (15 and 48%), leaves (39 and 0.7%), minerals (stones, earth; 4.3 and 1.1%), and small proportions of flowers, roots, fungus, seedlings, and invertebrates (insects, Order Coleoptera), each <1% of total dry weight. Curassows fed on 26 plant species from 21 families. When food resources for frugivores are scarce during the dry season (Nov–Apr), 47–50% of the diet was a single species (*Guazuma ulmifolia*, Sterculiaceae) indicating this species can be critical for curassow survival. An increase in consumption of leaves and invertebrates was observed in the rainy season (May–Jul). Most seeds observed in feces (93%; n = 5,408; range = 1–10 mm) were intact suggesting that curassows could have an important role as seed dispersers in this tropical ecosystem. *Received 20 November 2007. Accepted 10 April 2008.*

Food is important in the life history of most organisms. Thus, identification of key food resources of a particular species can assist in revealing its habits and behavioral patterns, and its ecological role in the community. This knowledge is also important when selecting conservation areas for endangered species (Jímenez et al. 2001).

Cracids are the most threatened family of birds in the Americas (Brooks and Strahl 2000, Brooks 2006); data on diet and feeding habits of this group have been reported for only a few species. Cracids are considered mainly herbivorous, consuming fruits, seeds, and leaves (Delacour and Amadon 2004). Curassows, in particular, appear to consume mostly fruits and seeds but occasionally feed on flowers, leaves, invertebrates, and soil (*Mitu salvini*, Santamaria and Franco 1994, 2000; Jiménez et al. 1998; Yumoto 1999; *M. mitu*, Torres 1989; *M. tuberosa*, Gutiérrez 1997; *Crax alector*, Érard and Sabatier 1989, Érard et al. 1991, Érard and Théry 1994, Théry et al. 1994; *C. rubra*, Sermeño 1997). The diet of curassows may vary throughout the year but fruit consumption is typically high (Érard et al. 1991, Santamaría and Franco 2000). Variation in consumption of fruits, seeds, and invertebrates has been detected on a daily basis for *Mitu salvini* and *Crax alector* (Jímenez et al. 1998, 2001). Unfortunately, few data are available to describe general patterns.

Identifying curassow food resources is relevant to understanding the role these species have in the dynamics of forest ecosystems. Cracids comprise an important component of the biomass of avian communities in neotropical ecosystems (Terborgh 1986a, Strahl and Grajal 1991). They also may constitute key elements in maintenance of plant communities (Begazo and Bodmer 1998), as many curassow species move considerably while feeding, and defecate or regurgitate intact seeds (Wenny 1993, Caziani and Protomastro 1994, Yumoto 1999, Mamani-F 2001). The decline of many curassow populations has caused concern for possible effects of their extinction on structure and dynamics of neotropical forests (Levey 1994).

The Yellow-knobbed Curassow (*Crax daubentoni*) occurs locally in the Llanos, dry woodlands, and gallery and deciduous forests in northern Venezuela and adjacent Colombia, being one of larger frugivores within its distribution (Schäefer 1953, Strahl and Silva 1997, Hilty 2003, Delacour and Amadon 2004). Buchholz and Bertsch (2006) desig-

[1] Laboratorio de Conservación y Manejo de Fauna, Departamento de Biología de Organismos, Universidad Simón Bolívar, Apartado 89000, Caracas 1080-A Venezuela.

[2] Corresponding author; e-mail: daubentoni@gmail.com

nated the status of *C. daubentoni* as Globally Vulnerable (VU A3a, c, d) due to accelerated urban and agrarian growth in northern Venezuela, and increasing hunting pressure. However, little is known about the status, biology, habitat requirements, and feeding habits of this species (Delacour and Amadon 2004).

Our objectives were to: (1) identify the composition and diversity of the diet of Yellow-knobbed Curassows in central Venezuela, and (2) examine its ecological role as possible dispersers of the plants they consume.

METHODS

Study Area.—The study was conducted on a 75,000-ha private cattle ranch (Hato Piñero, 08° 56′ N, 68° 05′ W) in the central Llanos of Venezuela (State of Cojedes) from November 2001 to July 2002. The study area included savannas, pastures, and deciduous dry and gallery forests. The specific study area was a 30,000-ha dry forest at the center of the ranch. The average annual temperature and precipitation are 27.5° C and 1,469.6 mm, respectively. There is strong seasonality with a rainy season (Apr–Nov) and a dry season (Dec–Mar) (Barreto and Hernández 1988, Hato Piñero 2005). Different conservation practices (closure to hunting, fire control, protection of forested areas, and maintenance of corridors between pastures) have been established at this ranch since 1953. Consequently, healthy populations of many species occur, which has permitted development of an ecotourism program. The only other cracid species in this area is the Rufus-vented Chachalaca (*Ortalis ruficauda*).

Diet Composition and Diversity.—We estimated composition and diversity of curassow diets based on: (1) fecal analyses, and (2) direct observations in the field. Feces were collected and observations were made during eight field trips (15–20 days each) during November 2001 to July 2002 (except Jan). Diversity was estimated by identifying the different species comprising the diet of curassows. We also analyzed contents of 15 stomachs from specimens collected between 1961 and 1980 by personnel of the Estación Biológica de Rancho Grande Museum (Ministry of Environment) in different localities of the central Llanos (Portuguesa, Cojedes, and Guárico states) and northern Venezuela (Falcón State).

Fecal Analyses.—Feces were collected by searching the area around water sources used by curassows, and at feeding and resting sites. Fifteen samples were collected on a monthly basis (90 samples total; 45/season). No samples were collected in July due to extensive flooding which prevented location of intact feces. Fecal samples >2 m apart were selected whenever possible to increase the probability of originating from different individuals. Feces within a 2-m circle were considered one sample as they likely belonged to the same individual.

Samples were oven dried at 70° C for 72 hrs and dry mass was measured to the nearest 0.01 g. We separated and weighed the different items for further identification. Seeds were counted and their status (intact or damaged) recorded. We considered intact seeds as those not showing evident damage (e.g., broken seeds). We also measured the seeds and related their size to their status through regression analyses to test the suggestion by Santamaría and Franco (2000) that fate of consumed seeds (predated or dispersed) depends on their size.

Direct Observations in the Field.—Curassows are elusive and shy; it was rarely possible to track individuals for periods longer than 2 min. Occasionally we could follow individuals while foraging for 10–20 min. We recorded every food the birds consumed whenever possible during these events. We catalogued items as: seeds, leaves, fruits, flowers, and took samples for further identification. Occasionally, we observed curassows eating soil. This was recorded as soil. Monthly composition of the diet was expressed as percent of observations in which every item was recorded in relation to the total number of observations.

Stomach Contents Analyses.—Stomach contents were washed with water and sieved (1 mm). Items in each sample were separated under a stereoscopic microscope and catalogued as seeds, leaves, fruits (only in the case of *Guazuma* sp., the only fruit for which we could separate the seed from the pulp), flowers, animal material, minerals (pebbles of different sizes differing from soil which could not be identified in feces or stomach contents), etc. Both wet and dry mass of every compo-

TABLE 1. Proportion and frequency of foods in Yellow-knobbed Curassow feces (n = 90) and stomachs (n = 15), and proportion of observations in which each food category was recorded (n = 192 feeding bouts).

Food categories	% Total dry weight[a]		Frequency[b]		Field observations % (# of feeding bouts)
	Feces	Stomach contents	Feces	Stomach contents	
Fruits[c]	41.39	49.40	0.57	0.53	57.8 (111)
Seeds	15.35	48.20	0.92	1.00	16.7 (32)
Leaves	38.62	0.65	0.83	0.33	3.1 (6)
Minerals	4.30	1.07	0.59	0.40	8.9 (17)
Flowers	0.00	0.36	0.00	0.27	12.5 (24)
Animals	0.34	0.008	0.11	0.13	0.5 (1)
Seedlings & cotyledons	0.00	0.03	0.00	0.07	0.5 (1)
Roots	0.00	0.07	0.00	0.13	0.0 (0)
Fungi	0.00	0.004	0.00	0.07	0.0 (0)
Other[d]	0.00	0.21	0.00	0.47	0.0 (0)

[a] (Dry weight of each category/total dry weight) × 100.
[b] Proportion of feces or stomachs in which the food occurred (range = 0 to 1).
[c] Including fruits consumed with or without seeds.
[d] Unidentified material.

nent were measured to the nearest 0.01 g; items were identified to the species level whenever possible.

The data are expressed as percent dry weight (mass) of every item (leaves, fruits, seeds, flowers, animal material) in relation to total mass and frequency (proportion of feces or stomachs in which the item was present). We note the amount of fruit may be underestimated due to the difficulty of identifying pulp as a separate component. We correlated these variables (Pearson coefficient with arcsine transformed data) to investigate whether the heaviest components were also the more frequent. We compared proportions in feces with stomachs using a Spearman test. A significant correlation indicates items with higher proportions in feces will also have higher proportions in stomachs (Barreto et al. 1997). Statistical analyses were performed using STATISTICA (V. 5.0) software (Statsoft 1984–2008).

RESULTS

Fecal Analyses.—The diet of Yellow-knobbed Curassows was mostly fruits (41% dry weight), leaves (39%), seeds (15%), minerals (4%), and small proportions of flowers, roots, fungus, seedlings, and invertebrates (insects, Order Coleoptera), each <1% of total dry weight (Table 1). Fruits (mainly *Guazuma ulmifolia*) and leaves were abundant in the diet. *G. ulmifolia* seeds and minerals, although not important in terms of weight, were frequent in the diet.

Guazuma ulmifolia fruits were the most important item from December to April (dry season) and accounted for 45–82% of the total dry weight. Leaves became the main part of the diet (48–89% dry weight) with an increase in consumption of minerals in June (rainy season) (Fig. 1). We found 12 different seed morphotypes in feces of which four could be identified to species and one to Family. We found 5,815 seeds in the 90 feces analyzed with size ranging from 1 to 10 mm. Ninety-three percent (n = 5,408) were intact and the remainder were partially damaged. We did not find a relationship between damaged seeds and their size (R^2 = 0.2476; P = 0.15; n = 12); however, small seeds (1–5 mm) had a low percent of damage or no damage at all.

Direct Observations in the Field.—One hundred and ninety-two observations of foraging curassows were made from November 2001 to July 2002. Fruits (dry and fleshy) and seeds were consumed most frequently (Table 1). Dry fruits were mainly *G. ulmifolia* (26.6% of observations) and *Samanea saman* (7.8%). Fleshy fruits most frequently consumed were *Mangifera indica* (9.9%) and *Thalia geniculata* (9.4%) (Table 2). Most fleshy fruits were indehiscent (the seeds remain in the fruit after it has been shed from the parent plant). Curassows consumed a wide array of fruit shapes (round, ellipsoidal, cylin-

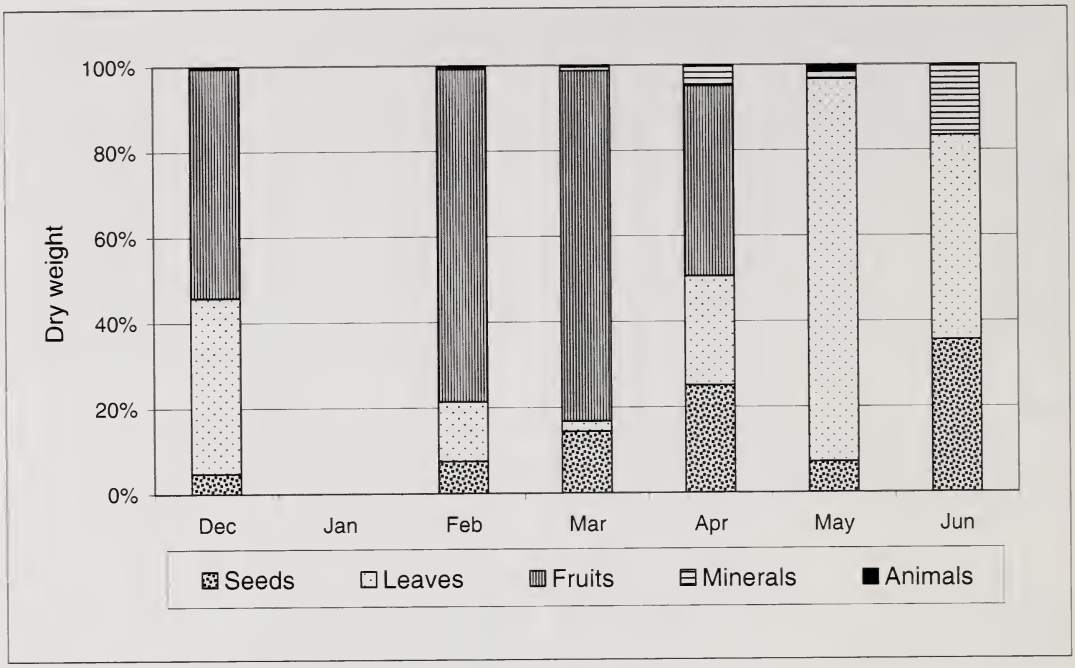


FIG. 1. Monthly variation in diet composition of Yellow-knobbed Curassows based on fecal analyses (n = 90). The number of fecal samples was 15/month.

drical, reniform, straight, curved), types (drupes and legumes), and colors (green, brown, yellow, red, white, and orange) mainly from trees and shrubs and, less frequently, from herbs. Curassows also ingested soil and pebbles (8.8%). All other components appeared in <5% of observations. Curassows were observed consuming seeds and seedlings embedded in livestock feces, and a curassow was observed consuming the tail of an unidentified lizard. Curassows were observed throughout the study (Nov–Jul) eating mainly fruits (Fig. 2). Seeds were observed being eaten from February to April. Both seedlings and animal material were consumed during the rainy season.

Stomach Content Analyses.—Stomachs contained mainly fruits and seeds with *G. ulmifolia* representing nearly 50% dry weight of the diet. Other components represented <1% dry weight (Table 1) including leaves from *Hecastotemon completus* and *Capparis odoratissima*, flowers of a Caesalpinaceae, and root fragments of an unidentified herb. A piece of a *Dyscomicetes* fungus was detected in one stomach. We found 13 morphotypes of seeds, seven identified to species and three to Family. Seed size ranged from 1 to 20 mm. *G. ulmifolia* and an unidentified Euphorbiaceae were the most frequent and dominant dry weight components (Pearson; r^2 = 0.22; P = 0.008; n = 31). Stomach contents differed from fecal contents (Spearman; R = 0.70; gl = 8; P = 0.19) although both stomachs and fecal contents had *G. ulmifolia* as the most important item. Stomachs contained more seeds, but fewer leaves, compared to feces.

Diet Diversity.—The diet of curassows included 26 plant species in 21 families in the Hato Piñero. Overall, curassows consumed 48 plant species in 29 families (Table 2). Thirty-six types of plant parts could be identified (25 to species, 6 to genus, and 5 to Family). Of these, 16 species provided fruits, 17 seeds, 10 flowers, 6 leaves, and 1 seedling. Legumes (8 species) were most frequently represented in the diet followed by Rubiaceae, Verbenaceae, and Boraginaceae (2 species each). Species consumed varied throughout the study period (Fig. 3).

DISCUSSION

Diet Composition.—Yellow-knobbed Curassows are frugivorous based on fecal and

TABLE 2. Diet of Yellow-knobbed Curassows in the Llanos of Venezuela based on fecal and stomach analyses, and field observations.

Family and species	Food category[a,c]	Found in[b,d]
Family Mimosaceae		
Acacia glomerosa	Se[c]	Ob, Fe
cv. *Mimosa pellita*	Se[c]	Fe
Enterolobium cyclocarpum	Se, S&C	Ob, Sc[d]
Samanea saman	Fr, Se, Fl	Ob, Sc
Family Bignoniaceae		
Arrabidaea mollisima	Le	Ob
Sp 1 Not identified	Se	Sc
Sp 2 Not identified	Se	Sc
Family Verbenaceae		
Lantana camara	Fr, Fl	Ob
L. trifolia	Fr, Fl	Ob
Family Rubiaceae		
cv. *Guettarda* sp.	Se[c]	Sc
Genipa americana	Fr, Le, Se	Ob, Fe[d]
Family Boraginaceae		
Cordia sp.	Fl	Ob
Cordia tetranda	Fr	Ob
Family Caesalpiniaceae		
Caesalpinia coriaria	Fr	Ob
Sp 1 Not identified	Fl	Sc
Family Sterculiaceae		
Guazuma ulmifolia	Fr	Fe, Sc, Ob
Family Marantaceae		
Thalia geniculata	Fl, Fr	Ob
Family Nyctacinaceae		
Guapira olfersiana	Le	Ob
Family Sapindaceae		
Allophylus racemosus	Fr, Le	Ob
Family Apocynaceae		
Tabernaemontana cymosa	Fr, Le	Ob
Family Combretaceae		
Combretum alternifolium	Fr, Fl	Ob
Family Flacourtiaceae		
Hecatostemon completus	Fr, Le	Ob, Sc
Family Rhamnaceae		
Zyzyphus cyclocordia	Fr	Ob
Family Anacardiaceae		
Mangifera indica	Frp	Ob
Family Chrysobalanaceae		
Licania pyrifolia	Frp	Ob
Family Capparidaceae		
Capparis odoratissima	Fr, Fl, Le	Ob, Sc
Family Arecaceae (Palmae)		
Copernicia tectorum	Fr	Ob
Family Alismotaceae		
Echinodorus paniculatus	Fr	Sc
Family Polygonaceae		
Coccoloba caracasana	Se	Ob, Sc
Family Cecropiaceae		
Cecropia sp.	Fl	Ob
Family Fabaceae		
cv. *Sesbania* sp.	Se[c]	Sc
Family Convolvulaceae		
cv. *Convolvus* sp.	Se[c]	Sc
Family Passifloraceae		
cv. *Passiflora* sp.	Se[c]	Sc
Family Cyperaceae		
cv. *Scleria* sp.	Infrut	Sc
Family Euphorbiaceae		
Sp 1 not identified	Se[c]	Sc
Family Poaceae		
Sp 1 not identified	Fr	Fe

[a] Se = Seed; Fr = Fruits (including seeds); Frp = Fruit pulp (seeds not consumed); Infrut = Infrutescence; Fl = Flowers; L = Leaves; S&C = Seedlings and Cotyledons.
[b] Ob = field observation; Fe = Feces; Sc = Stomach content.
[c] Not certain if the seed was consumed alone or with the fruit.
[d] Not certain about the identification of the item.

stomach content analyses, and direct observations in the field. They also consumed seeds, leaves, flowers, roots, fungi, animal matter, and soil as reported for other curassows (Torres 1989, Érard et al. 1991, Calchi and Pérez 1997, Gutiérrez 1997, Renjifo and Renjifo 1997, Santamaría and Franco 2000, Jímenez et al. 2001).

Fruits, the most frequently ingested food item, are nutritious and high energy foods. They represent a rich source of carbohydrates while seeds (most consumed with the fruit) contain protein and lipids (Howe and Westley 1988). Despite these features, it is not clear which traits present in fruits affect their choice by birds (reviewed by Levey and Martínez del Río 2001). Leaves are low calorie foods that are difficult to digest due to high content of structurally complex carbohydrates, including cellulose, hemicellulose and pectins, phenolic polymers such as lignin and tannins, and a variety of toxic secondary compounds including alkaloids, terpenoids, and cyanogenic compounds (Howe and Westley 1988). These compounds make leaves a low-intake item for birds. Morton (1978) and Jimenez et al. (2001) observed that consumption of leaves for nutrients (e.g., nitrogen) can be expected in frugivorous birds. Galliformes (Cracidae, Phasianidae) are among birds which feed upon leaves most frequently with some species entirely foliovorous (*Lagopus*, *Canachi-*

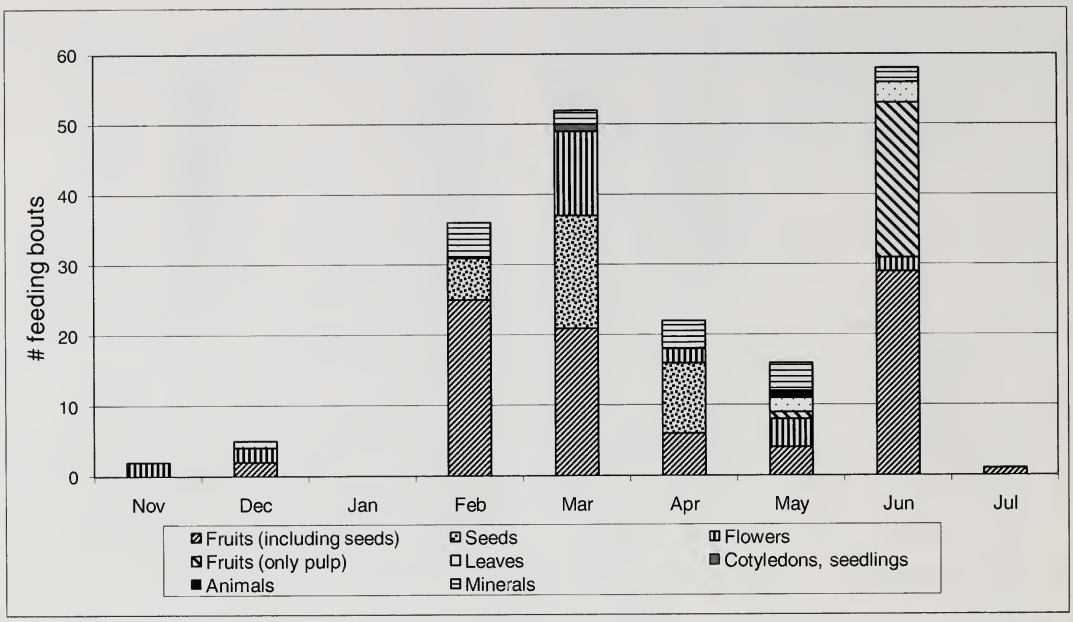


FIG. 2. Monthly variation in diet composition of Yellow-knobbed Curassows based on field observations (n = 192 feeding bouts). Number of observations differed between months and is represented by the monthly number of feeding bouts.

Species	Months								
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Thalia geniculata	----------	----------	...?...	----------	----------	----------	----------		
Guazuma ulmifolia		----------	...?...	----------	----------	----------	----------		
Acacia glomerosa		----------	...?...	----------	----------	----------	----------		
Guapira olfersiana				----------					
Enterolobium cyclocarpum				----------	----------	----------	----------		
cv. *Mimosa pellita*				----------	----------	----------	----------		
Coccoloba caracasana				----------	...?...	----------			
Hecatostemon completus				----------				----------	
Caesalpinia coriaria					----------	----------	----------		
Combretum alternifolium					----------	----------	----------		
Samanea saman					----------	----------			
Capparis odoratissima					----------	...?...	----------	----------	
Poaceae sp. 1							----------		
Genipa americana							----------	----------	
Lantana camara							----------	----------	
Licania pyrifolia							----------	----------	
Arrabidaea mollisima							----------	----------	
Allophylus racemosus							----------	----------	----------
Lantana trifolia								----------	
Cordia sp.								----------	
Zyzyphus cyclocordia								----------	
Mangifera indica								----------	
Copernicia tectorum								----------	
Cordia tetranda								----------	
Cecropia sp.								----------	
Tabernaemontana cymosa								----------	

...? = even when it was not observed for that period, it is probable the item was consumed, because we observed curassows eating it during the month before and after.

FIG. 3. Monthly variation in diet diversity (species or Family level) of Yellow-knobbed Curassows based on field observations and fecal analysis.

tes, and *Tetrao*; Morton 1978). Some species of cracids are reported to feed on leaves: the diet of *Mitu mitu* is 68% leaves in Perú (Torres 1989), and leaves comprised 39 and 27% of the diet of *Ortalis canicolis* and *Penelope perspicax* in Argentina and Colombia, respectively (Caziani and Protomastro 1994, Muñoz 2004).

Consumption of soil (geophagy) by animals has been attributed to requirements for specific nutrients, anti-acids, or detoxifying substances, or to enhance grinding of food in the gizzard (Diamond et al. 1999). Soil comprised 2–10% of the diet of cracids. Nine percent of the birds we observed ingested soil and it comprised 1 and 4% dry weight in stomachs and feces, respectively. Curassows have been observed eating small pebbles which may be related to the need to grind material inside their strong gizzard (Delacour and Amadon 2004).

Several species of cracids have been reported to consume animal material including insects (ants, butterflies, caterpillars; Caziani and Protomastro 1994), earthworms (Érard et al. 1991, Érard and Théry 1994, Arriaga and Bermúdez 1997, Gutiérrez 1997, Renjifo and Renjifo 1997), spiders, terrestrial crabs, and snails (Santamaría and Franco 2000), live adult frogs, lizards, and snakes (Torres 1989), bird eggs, chicks, and carcasses of armadillos (*Dasypus* sp.), pacas (*Cuniculus paca*), rats (a number of Muridae species), and bats (Chiroptera) (Renjifo and Renjifo 1997, Santamaría and Franco 2000). This consumption, in all reported cases, coincided with the reproductive period when adults feed chicks a high protein-based diet (Morton 1973). We found small quantities of animal material (0.52% of observations and <1% dry weight in both feces and stomachs). This material may have been consumed incidentally while eating fruits, although it coincided with hatching of eggs in April (Kvarnbäck et al. 2008).

Seeds as a separate item from fruit may be overestimated as it is difficult to recognize fruit pulp in stomachs or feces. Our observations indicate curassows ingest mainly fruits, but were observed eating seeds on a few occasions. Thus, the importance of seeds in feces or stomachs (Table 1) may be an artifact, underestimating the real importance of fruits in the diet.

Different methods (fecal and stomach analyses, and direct observations) produced different results concerning importance of components other than fruits (Fig. 4). Fecal analyses produced proportions of seeds and leaves inverse from those resulting from stomach analyses. A richer diet was revealed by stomach content analysis compared to any other method, partially because the food is less processed making it possible to distinguish features that are not distinguishable in feces. However, stomach analysis requires collecting the animal.

Diet Seasonality.—The diet of Yellow-knobbed Curassows varied throughout the year with a predominance of legumes and dry fruits during the dry season, and a shift to drupes, flowers, leaves, and small proportions of animal material during the rainy season. Food resources and water are scarce during the dry season, which is a particularly difficult time for frugivorous, folivorous, and insectivorous animals (Robinson 1986, Niño P 1994). Curassows consumed large quantities of *G. ulmifolia* during the dry season, one of the few species with fruits at this time of the year, as most species produce fruits by the onset of the rainy season (Robinson 1986; pers. obs.). *G. ulmifolia*, a common species in the Llanos, is consumed by a number of frugivores and has been reported as the most important item in the diet of peccaries (*Tayassu* spp.) in the study area (Barreto et al. 1997); *G. ulmifolia* represents a keystone species in this environment (*sensu* Terborgh 1986b). Other cracids have also been reported to depend on key plant species: *Mitu mitu* in Perú (4 species of Moraceae: *Brosinum* sp., *Clarisia racemosa*, *Ficus* sp., and *Pseudolmenia* sp.) (Torres 1989), *M. salvini* in Colombia (*Guarea guidonia*) (Santamaría and Franco 2000), and *Ortalis canicollis* in Argentina (*Schinus poygamus* and *Rivina humilis*) (Caziani and Protomastro 1994).

Availability of resources is higher during the rainy season and curassows had a diverse diet during that period. It is possible that curassows behave as opportunistic foragers, consuming a wide array of resources as they become available. Curassows were observed shifting foraging areas if they contained more seeds, leaves, flowers, and fruits (Bertsch and Barreto 2008).

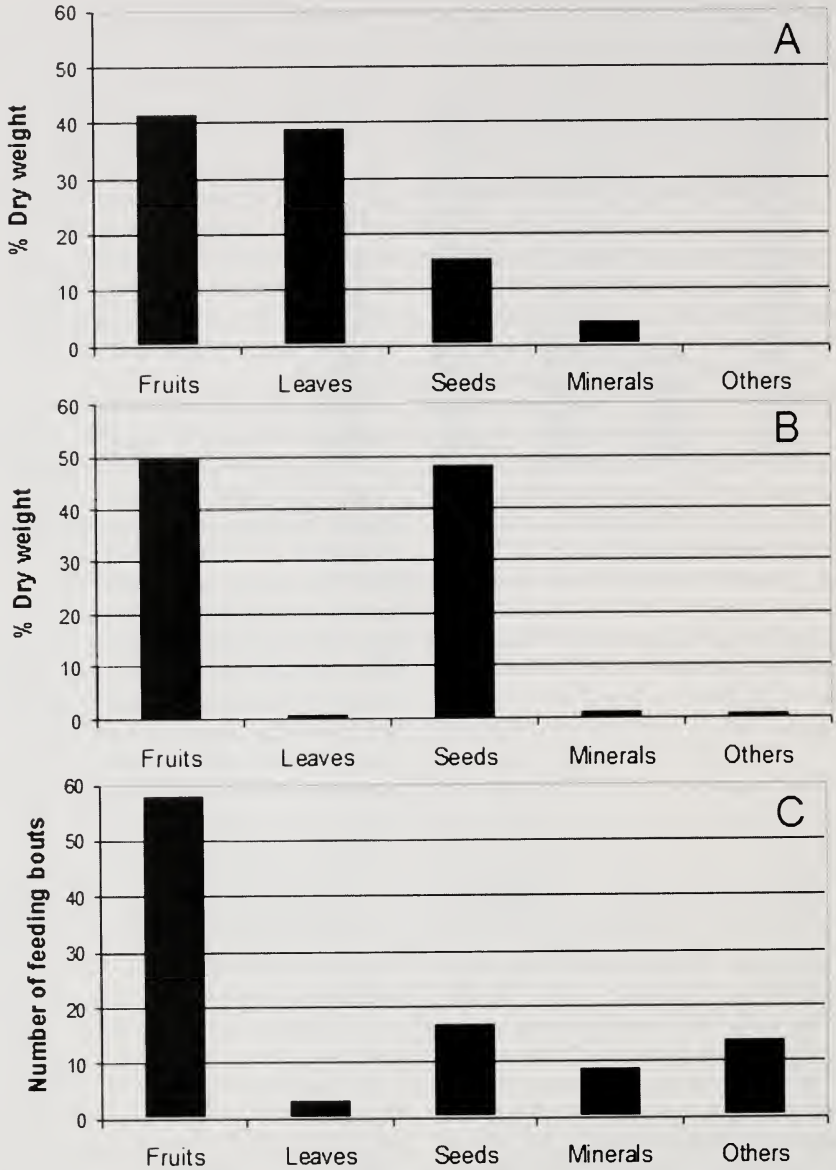


FIG. 4. Food categories in the diet of Yellow-knobbed Curassows: feces (A), stomach analysis (B), and field observations (C).

Seed Dispersers or Predators?—Are curassows dispersers or predators of the seeds they consume? Too few data are available to properly answer this question. Diets vary among species (Levey 1994, Théry et al. 1994) with guans and chachalacas serving as efficient seed dispersers (Terborgh 1986a, Strahl and Grajal 1991, Wenny 1993, Caziani and Protomastro 1994, Mamani-F 2001, Brooks and Fuller 2006), while curassows serve as dispersers and predators (Érard and Sabatier 1989, Érard and Théry 1994, Yumoto 1999). The difference may be attributed to their digestive physiology, as guans and chachalacas can regurgitate seeds they consume and have relatively weaker gizzards than those of curassows, leaving seeds to pass intact through their digestive tract (Delacour and Amadon

2004). Some studies suggest that seed size can affect seed fate. Larger seeds (6–30 mm) were completely destroyed in the gastrointestinal tracts of *Mitu salvini* and *Crax alector* compared to smaller (2–5 mm) seeds (Yumoto 1999, Santamaría and Franco 2000). Larger seeds comprised most of the diet of these species, making them seed predators, but they occasionally ingested smaller seeds which were dispersed. Seeds consumed by *C. daubentoni* in our study were mostly intact in feces, especially those <1–5 mm, in agreement with Santamaría and Franco (2000). Preliminary experiments showed that seeds of *G. ulmifolia* and *S. saman* germinated after passing through the digestive tract of birds, suggesting the Yellow-knobbed Curassow may be an important disperser of some of the plants they consume.

This study demonstrated that, although *C. daubentoni* has been considered a forest dwelling species (Schäefer 1953); it also uses resources at the forest border (e.g., *G. ulmifolia*) and open areas (e.g., *Mangifera indica*, *Licania pyrifolia*). The current habitat of the Yellow-knobbed Curassow is highly fragmented, and this behavior may be advantageous if this species is tolerant of fragmentation (Strahl and Grajal 1991, Borges 1999). Illegal hunting may be the most serious factor threatening Yellow-knobbed Curassow populations throughout their range.

ACKNOWLEDGMENTS

We thank the owners and personnel of Hato Piñero for facilities and allowing us to conduct this study on their property. We also thank Gertrudis Gamarra for assistance in the field. John Kvarnbäck, Gabriela Echevarria, Loto Kanta Chandra, Oskar Nilsson, Alejandro Nagy, and Francia Medina helped in the field during different times. Francisco Delascio and Elizabeth Pérez helped identify botanical samples. Francisco Bisbal from Estación Biológica de Rancho Grande kindly lent the stomach samples. Comments by Carlos Bosque, Dan Brooks, Pablo Lau, Doug Levey, and Virginia Sanz were useful in clarifying our ideas. This Project was possible thanks to the financial support of Fundación Branger and Organización para Estudios Tropicales (OET) in Costa Rica.

LITERATURE CITED

Arriaga, I. and S. Bermúdez. 1997. Dieta de la Guacharaca (*Ortalis ruficauda*) en el Estado Cojedes. Pages 34–47 *in* The Cracidae: their biology and conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House Publishers, Blaine, Washington, USA.

Barreto, G. R. and O. E. Hernández. 1988. Aspectos bioecológicos de los Báquiros (*Tayassu tajacu* y *T. pecari*) en el Estado Cojedes: estudio comparativo. Thesis. Universidad Central de Venezuela, Caracas.

Barreto, G. R., O. E. Hernández, and J. Ojasti. 1997. Diet of peccaries (*Tayassu tajacu* and *T. pecari*) in a dry forest of Venezuela. Journal of Zoology (London) 241:279–284.

Begazo, A. and R. Bodmer. 1998. Use and conservation of Cracidae (Aves: Galliformes) in the Peruvian Amazon. Oryx 32:301–309.

Bertsch, C. and G. R. Barreto. 2008. Abundancia y área de acción del paují de copete (*Crax daubentoni*) en los llanos centrales de Venezuela. Ornitología Neotropical 19:287–293.

Borges, S. H. 1999. Relative use of secondary forests by cracids in central Amazonia. Ornitología Neotropical 10:77–80.

Brooks, D. M. (Editor). 2006. Conserving cracids: the most threatened family of birds in the Americas. Miscellaneous Publication Number 6. Houston Museum of Natural Science, Houston, Texas, USA.

Brooks, D. M. and R. A. Fuller. 2006. Biology and conservation of cracids. Pages 9–21 *in* Conserving cracids: the most threatened family of birds in the Americas (D. M. Brooks, Editor). Miscellaneous Publication Number 6. Houston Museum of Natural Science, Houston, Texas, USA.

Brooks, D. M. and S. D. Strahl. 2000. Curassows, guans and chachalacas. Status survey and conservation action plan for cracids 2000–2004. IUCN, Gland, Switzerland.

Buchholz, R. and C. Bertsch. 2006. *Crax daubentoni*. Pages 91–94 *in* Conserving cracids: the most threatened family of birds in the Americas (D. M. Brooks, Editor). Miscellaneous Publication Number 6. Houston Museum of Natural Science, Houston, Texas, USA.

Calchi, R. and N. Pérez. 1997. Notas sobre dos especies pertenecientes a la Familia Cracidae. Page 12 *in* The Cracidae: their biology and conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House Publishers, Blaine, Washington, USA.

Caziani, S. and J. Protomastro. 1994. Diet of the Chaco Chachalaca. Wilson Bulletin 106:640–648.

Delacour, J. and D. Amadon. 2004. Curassows and related birds. Second Edition. Lynx Edicions and American Museum of Natural History, Barcelona, Spain and New York, USA.

Diamond, J., K. D. Bishop, and J. D. Gilardi. 1999. Geophagy in New Guinea birds. Ibis 141:181–193.

Érard, C. and D. Sabatier. 1989. Rôle des oiseaux frugivores terrestres dans la dynamique forestière

en Guyane française. Proceedings of the International Ornithological Congress 19:803–815.

ÉRARD, C. AND M. THÉRY. 1994. Frugivorie et ornithochorie en forêt guyanaise: l'éxemple des grands oiseaux terrestres et de la *Penelope marail*. Alauda 62:27–31.

ÉRARD, C., M. THÉRY, AND D. SABATIER. 1991. Régime alimentaire de *Tinamus major* (Tinamidae), *Crax alector* (Cracidae) et *Psophia crepitans* (Psophiidae), en forêt guyanaise. Gibier Faune Sauvage 8:183–210.

GUTIÉRREZ, R. 1997. Observaciones de la población de *Mitu tuberosa* (Linnaeus, 1766) en el Parque Nacional El Manu, Perú. Pages 80–88 *in* The Cracidae: their biology and conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House Publishers, Blaine, Washington, USA.

HATO PIÑERO. 2005. Wildlife paradise-Venezuela. http: // www.hatopinero.com (accessed 2 December 2005).

HILTY, S. 2003. Birds of Venezuela. Christopher Helm Publishers, London, United Kingdom.

HOWE, H. AND L. WESTLEY. 1988. Ecological relationships of plants and animals. Oxford University Press, New York, USA.

JIMÉNEZ, I., J. ALDANA, C. D. CADENA, AND J. FORERO. 1998. How does the diet of a curassow vary within a week? Field Studies of New World Monkeys, La Macarena, Colombia 12:33–40.

JIMÉNEZ, I., J. L. PARRA, M. AGUDELO, G. LONDOÑO, AND Y. MOLINA. 2001. Temporal variation in the diet of Black Curassows (*Crax alector*, Cracidae). Pages 195–211 *in* Cracid ecology and conservation in the new millenium (D. M. Brooks and F. Gonzalez-Garcia, Editors). Miscellaneous Publication Number 2. Houston Museum of Natural Sciences, Houston, Texas, USA.

KVARNBÄCK, J., C. BERTSCH, AND G. R. BARRETO. 2008. Nest-site selection and nesting success of the Yellow-knobbed Curassow (*Crax daubentoni*) in a fragmented landscape in the Venezuelan llanos. Ornitología Neotropical 19:347–352.

LEVEY, D. 1994. Cracids as seed dispersers: what we need to know and why it is important. Cracid Newsletters 3.

LEVEY, D. AND C. MARTÍNEZ DEL RÍO. 2001. It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. Auk 118:819–831.

MAMANI-F., A. M. 2001. Historia natural y evaluación de la densidad poblacional de *Ortalis canicollis* (Charata) en Izozog, Provincia Cordillera del Dpto. Santa Cruz, Bolivia. Pages 87–100 *in* Cracid ecology and conservation in the new millennium (D. M. Brooks and F. Gonzalez-Garcia, Editors). Miscellaneous Publication Number 2. Houston Museum of Natural Sciences, Houston, Texas, USA.

MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. American Naturalist 107:8–22.

MORTON, E. S. 1978. Avian arboreal folivores: why not? Pages 123–130 *in* The ecology of arboreal folivores (G. G. Montgomery, Editor). Smithsonian Institution Press, Washington, D.C., USA.

MUÑOZ, M. 2004. Características morfológicas, nutricionales y de disponibilidad de los frutos en la dieta de *Penelope perspicax* (Aves, Cracidae), en el Santuario de Flora y Fauna Otún, Colombia. Boletín del Grupo de Especialistas en Crácidos. Number 19.

NIÑO P., I. O. 1994. Correlaciones de estructura y preferencia de hábitat del Paují Copete de Plumas (*Crax daubentoni*) en los llanos del Estado Guárico. Thesis. Universidad Central de Venezuela, Caracas.

RENJIFO, J. AND J. T. RENJIFO. 1997. *Pauxi unicornis*: biología y ecología. Pages 89–92 *in* The Cracidae: their biology and conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House Publishers, Blaine, Washington, USA.

ROBINSON, J. G. 1986. Seasonal variation in use of time and space by wedge-capped capuchin monkey *Cebus olivaceus*: implications for foraging theory. Smithsonian Contributions to Zoology Number 431.

SANTAMARIA, M. AND A. M. FRANCO. 1994. Historia natural del Paujil *Mitu salvini* y densidades poblacionales de Crácidos en el Parque Nacional Natural Tinigua-Amazonia Colombiana. Informe Final. Wildlife Conservation Society, Bogata, Colombia.

SANTAMARIA, M. AND A. M. FRANCO. 2000. Frugivory of Salvin's Curassow in a rainforest of the Colombian Amazon. Wilson Bulletin 112:473–481.

SCHÄEFER, E. 1953. Estudio bio-ecológico comparativo sobre algunos Cracidae del norte y centro de Venezuela. Boletín de la Sociedad Venezolana de Ciencias Naturales 15:30–63.

SERMEÑO, A. 1997. Alimentación y reproducción del Paujil (*Crax rubra*) en El Salvador. Pages 71–79 *in* The Cracidae: their biology and conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House Publishers, Blaine, Washington, USA.

STATSOFT INC. 1984–2008. Statistica v 5.0. Statsoft Inc., Tulsa, Oklahoma, USA.

STRAHL, S. D. AND A. GRAJAL. 1991. Conservation of large avian frugivores and the management of neotropical protected areas. Oryx 25:50–55.

STRAHL, S. D. AND J. L. SILVA. 1997. The status of the Family Cracidae in Venezuela. Pages 383–393 *in* The Cracidae: their biology and conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House Publishers, Blaine, Washington, USA.

TERBORGH, J. 1986a. Community aspects of frugivory in tropical forests. Pages 371–383 *in* Frugivores and seed dispersal (A. Estrada and T. H. Fleming, Editors). Dr. W. Junk Publishers, The Hague, Netherlands.

TERBORGH, J. 1986b. Keystone plant resources in the

tropical forest. Pages 330–344 *in* Conservation biology: the science of scarcity and diversity (M. Soulé, Editor). Sinauer Associates, Sunderland, Massachusetts, USA.

Théry, M., C. Emid, and D. Bati. 1994. Diets of the Marail (*Penelope marail*) and the Black Curassow (*Crax alector*). Cracid Newsletters 3.

Torres, B. 1989. La dieta del paujil (*Mitu mitu*): o las vicisitudes de ser frugívoro. Boletín de Lima 66: 87–90.

Wenny, D. 1993. Black Guans and seed dispersal in Costa Rica. Cracid Newsletters 2.

Yumoto, T. 1999. Seed dispersal by Salvin's Curassow, *Mitu salvini* (Cracidae), in a tropical forest of Colombia: direct measurements of dispersal distance. Biotropica 31:654–660.

The Wilson Journal of Ornithology 120(4):778–783, 2008

LANDSCAPE CONFIGURATION EFFECTS ON DISTRIBUTION AND ABUNDANCE OF WHIP-POOR-WILLS

MICHAEL D. WILSON[1,2] AND BRYAN D. WATTS[1]

ABSTRACT.—We examined the influence of landscape configuration created by forest regeneration practices on distribution of Whip-poor-wills (*Caprimulgus vociferous*) during the breeding season by comparing relative abundance and space use between forest areas (stands ≥ 17 years of age) and regenerating forest edges (regeneration stand ≤ 6 years of age adjacent to forest area). Regenerating forest edges contained greater ($P < 0.001$) abundance of Whip-poor-wills ($\bar{x} \pm SE = 2.4 \pm 0.30$ birds/10 ha) than forest areas (0.8 ± 0.11 birds/10 ha). Eighty-four percent of detections at regenerating forest edges were from within the regenerating stand. However, Whip-poor-wills within regenerating stands were detected within 100 m of the forested edge with a greater probability ($P < 0.001$) than expected by chance. The positive response of Whip-poor-wills to forest edges is likely due to proximity and use of foraging habitats. The relatively high number of habitat openings created by some forest regeneration practices provide Whip-poor-wills with foraging opportunities not present in less intensively managed forest systems. Forest management for Whip-poor-wills should consider harvest strategies that maintain the availability of regenerating patches in close proximity to mature forests. *Received 18 August 2006. Accepted 30 January 2008.*

The distribution and abundance of species that depend on resources that are not contained within a single patch type are likely influenced by the spatial organization of all required habitat types (Szaro and Jackle 1985, Dunning et al. 1992, Pearson 1993, Watts 1996, Sisk et al. 1997, Ries and Sisk 2004). This is because species that depend on more than one habitat type must broaden their use of a landscape to include all patch types needed to meet their requirements. The use of a habitat patch within a heterogeneous landscape for these species is influenced both by the characteristics of the patch (e.g., food supply, predation risk, competitive pressure, behavioral constraints) and the characteristics of surrounding patches (Hansson 1977, Foster and Gaines 1991, Johnson et al. 1992, Rodewald and Yahner 2001). Ultimately it is likely that spatial association of required habitat patches serves as the most important characteristic in affecting distribution and abundance of a species in a landscape (Szaro and Jackle 1985, Dunning et al. 1992, Pearson 1993, Watts 1996, Sisk et al. 1997, Ries and Sisk 2004).

Whip-poor-wills (*Caprimulgus vociferous*) are nocturnal insectivorous birds that typically nest in forested habitat but frequently use open habitats including fallow fields, cropland, shrubland, and regenerating pine (*Pinus* spp.) stands for foraging (Bent 1940, Cooper 1981, Eastman 1991, Peterjohn and Rice 1991). That Whip-poor-wills use resources that can occur in distinctly different habitat types implies their distribution and abundance may be influenced by the spatial configuration of patches within a broader landscape. Thus, Whip-poor-will abundance would be predicted to respond positively to landscapes where the required patches are in close proximity (Ries and Sisk 2004).

Forested landscapes under intensive management often contain a spatial mosaic of different age stands where adjacent stands (i.e., patches) are separated by abrupt edges (Thompson et al. 1995). Landscapes that are frequently disturbed by forest regeneration practices may provide Whip-poor-wills with habitat opportunities not available in less-intensively managed forest systems. The objective of our study was to investigate the effect of the spatial arrangement of habitat patches created by regeneration forest management on the distribution and abundance of Whip-poor-wills.

METHODS

Study Area.—Our study was conducted on a 30,000 ha forested tract in eastern North Carolina (~35° 30′ N, 76° 60′ W) that is managed primarily as a loblolly pine (*Pinus taeda*) plantation. The tract is divided among 1,010

[1] Center for Conservation Biology, College of William and Mary, Williamsburg, VA 23187, USA.

[2] Corresponding author; e-mail: mdwils@wm.edu

forest stands that are individually managed on a 30–35 year rotation schedule. Pine stands were initially planted as seedlings in parallel rows with a stocking level of 800 to 1,200 pine stems/ha. Young regenerating stands (1–5 years after planting) are characterized by a dense cover of shrubby plants, a high percentage of ground cover of grasses and forbs, and no overstory (i.e., open). Dominant plants include switch cane (*Arundinaria gigantea*), sweet pepperbush (*Clethra anifolia*), highbush blueberry (*Vaccinium corymbosum*), and blackberry (*Rubus sp.*). Pines reach a height of ~2.5 m after 6 years. Stands are commercially thinned two times (at ~12–15 years and 19–21 years after planting) before final harvest. Mature stands are characterized by dense understory vegetation dominated by switch cane, sweet pepperbush, highbush blueberry, fetterbush (*Lyonia lucida*), and gallberry (*Ilex glabra*). Dominant hardwood trees include red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), red bay (*Persea borbonia*), sweet bay (*Magnolia virginiana*), and tulip poplar (*Lirodendron tulipifera*). Mature stands are harvested by clear-cutting. A network of logging roads cross the landscape. The staggered regime of harvesting and thinning creates a spatial mosaic of different age stands separated by distinct boundaries (Wilson and Watts 1999).

Study Design.—The influence of the configuration on stands of different age was examined by comparing the number of Whip-poor-wills at survey points along the boundary between two mature forest stands (forested area) to survey points along the boundary between one mature forest stand and one open, regenerating stand (regenerating edge). All mature forests had been planted 17–28 years prior and had been commercially thinned at least once. Regenerating stands were planted with pines within the last 1–5 years. Twenty-nine forested areas and 28 regenerating edges were selected as spatial replicates for study. Criteria for selection included stand size and shape. Small, narrow stands were avoided to reduce contagious effects from edges of other stands not selected for study. We selected a replicate for survey only if adjacent stands shared at least 350 m of edge. Each spatial replicate contained one point count station positioned on a logging road and along the edge between the two focal stands. The location of survey points was chosen to maximize the distance between the boundaries of other stands not selected for study.

Bird Surveys.—The 57 survey points were divided into two groups (31 and 26 points, respectively) that were sampled on different nights between 13 May and 17 July 1999. All points were visited seven times during this period. Whip-poor-will activity is known to vary with lunar light intensity (Mills 1986, Wilson and Watts 2006); thus the two groups of points were surveyed on sequential nights over different periods of the lunar phase (new moon, first quarter, full moon, last quarter). Surveys began at 0.5 hrs after dusk and ended at least 1 hr before sunrise, and were conducted by driving between points on a predetermined route. The order in which points were visited was reversed between successive visits to reduce bias due to time of night. Surveys were not conducted during rain or winds >15 km/hr. One observer stood at the survey point during each point visit and recorded all birds that performed at least one syllable of the onomatopoeic "whip-poor-will" vocalization for a period of 5 min. Surveys may be biased to detect calling males because females are not known to routinely use this specific vocalization (Cink 2002). Visual detections and other vocalizations, such as grunt calls (Cink 2002), were not recorded to avoid biasing counts near the road edge or by stand type. The positions of all birds were mapped so detections could be summarized by the distance from the observer, distance from the edge of the two focal stands, or distance from the edge of any other stand within the vicinity.

We attempted to verify the observer's accuracy of estimating the location of Whip-poor-wills from call-count surveys by comparing these data to locations estimated from radio-marked birds at this site the following year (Wilson 2003). This is not a direct measure an observer's ability to estimate location because it compares data collected independently, but we believe it offers the only opportunity to validate an observer's ability to identify the location of Whip-poor-wills at night. We summarized the estimated distance of Whip-poor-wills to the nearest forest edge for all observations in each data set into 100-m intervals and compared them for indepen-

dence using χ^2 analysis. There was no significant difference ($\chi^2_3 = 3.27$, $P > 0.10$) between locations estimated by using call counts and locations estimated by using radio telemetry. We assume that Whip-poor-wills used space in a consistent manner between years and this space use can be measured effectively using each technique.

Statistical Analyses.—Density values ($\bar{x} \pm$ SE) used to compare abundance between forest areas and regenerating edges were calculated using only the detections within a specified transect. The width of each transect was standardized among all survey points to limit detections used for this anaylsis to those observed within a 100 m perpendicular distance measured from the boundary between stands selected for study. The length of each transect was allowed to vary between individual survey points to concentrate the investigation within a zone between stands selected for study, and to eliminate observations that might have been influenced by other stand edges not selected for study. This was accomplished by changing the lengths of each transect so it terminated at a distance of 150 m from the edges between other stands not selected for study. The survey visit with the highest recorded abundance within each transect was used for the density estimate. Density values were standardized to number of birds/10 ha (i.e., 500 m length × 200 m width rectangular transect) before analysis to accommodate variation in transect length. Density was compared between edge types using a one-way ANOVA (Statistica 6.1, Statsoft Inc.1984–2005).

Whip-poor-will distribution was also compared between two stands that shared a common edge by summing all detections collected during the entire study into 100-m distance classes. This overall sum represents an accumulated pattern of space use through time rather than a population index since the samples are not independent. The total number of detections varied among survey nights due to changes in lunar light conditions (Wilson and Watts 2006). However, detection frequencies between distance classes were statistically indistinguishable across lunar conditions (i.e., <25%, 26–50%, and >50% of moon face illuminated) (3 × 2 contingency tables for all χ^2 values <4.5, all $P > 0.20$) and the data were pooled.

We also compared the influence of stand age on edge use (Whip-poor-will detections) between forested stands and regenerating stands using χ^2 contingency tables. We used detections for this comparison only within 100 m of the boundary between two adjacent focal stands. Stands of each forested area were randomly assigned to one of two groups for this comparison. We examined the influence of stand type on relative edge use by testing for independence between detections 0–100 m and 101–200 m from the edge of adjacent forested stands, and adjacent forest and regenerating stands using χ^2 contingency tables.

The distribution of Whip-poor-wills within regenerating stands was further examined by comparing the distance of all observations from the nearest forest edge to an expected random distance using χ^2 analysis. This comparison included the entire perimeter of the regenerating stand and not only the boundary that was selected for density comparisons. Distances were expected to vary geometrically with stand area and shape; thus, separate statistical comparisons were made from five stand size classes; (1) <20 ha ($n = 2$), (2) 21–30 ha ($n = 4$), (3) 31–40 ha ($n = 8$), (4) 41–50 ha ($n = 4$), and (5) stands ≥51 ha ($n = 10$). Expected values were generated by creating 30 random locations within each open stand from digitized stand maps using ArcView 3.2 GIS software (ESRI 1992) and the animal movement extension of Hooge et al. (1999). The distance of random points to the nearest stand edge was measured from GIS coverage. The distances of both observed and random locations from the nearest forested stand edge were classified by 100-m intervals before comparison.

RESULTS

Regenerating edges supported a significantly greater ($F_{1,55} = 27.6$, $P < 0.001$) average density of Whip-poor-wills compared to forested areas ($\bar{x} \pm$ SE, 2.4 ± 0.30 birds/10 ha and 0.8 ± 0.11 birds/10 ha, respectively). The distribution of Whip-poor-wills between adjacent stands was influenced by edge type ($\chi^2_1 = 46.4$, $P < 0.001$). The frequency of all Whip-poor-wills detected in forest areas was evenly distributed between adjacent mature

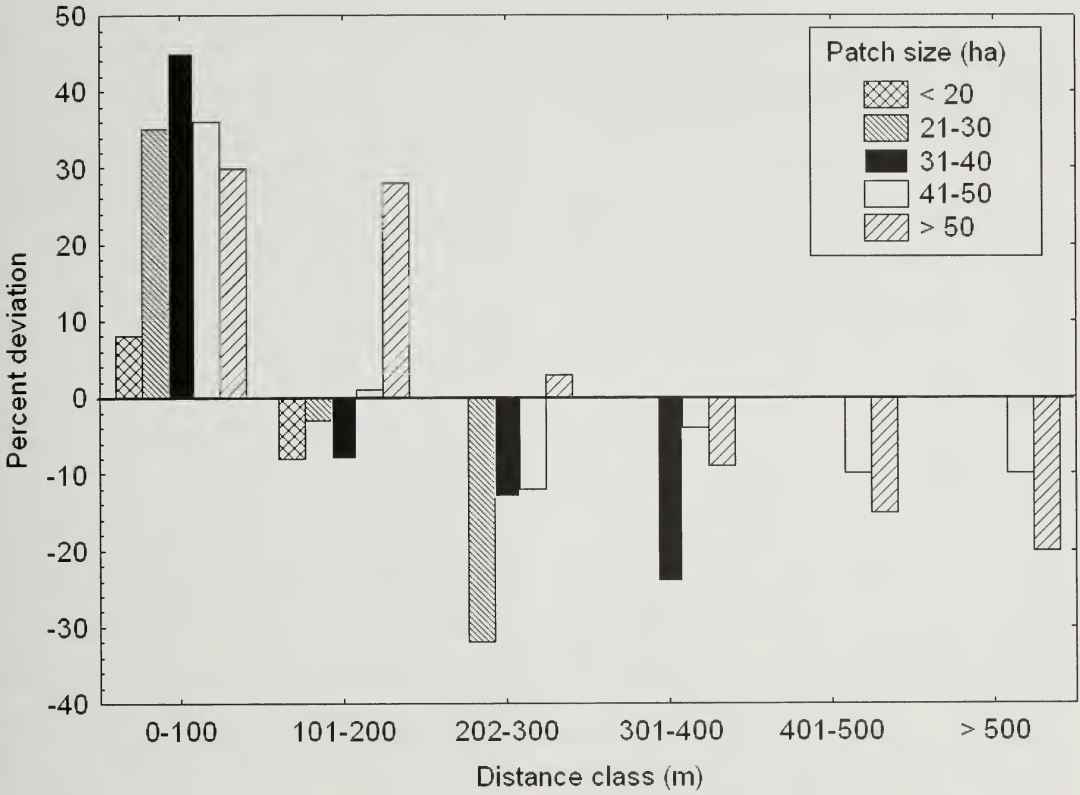


FIG. 1. Deviation (%) between observed locations of Whip-poor-wills within regenerating forest stands and an expected random distribution after classification into distance categories from the nearest forested edge. Positive deviations indicate distance categories where Whip-poor-wills were detected with greater frequency than expected by chance and negative deviations indicate the distance categories where Whip-poor-wills were detected less frequently than by chance.

forest stands ($\chi^2_1 = 0.74$, $P = 0.61$) with 45% and 55% of detections occurring in one of two randomly assigned groups, respectively. Whip-poor-wills in regenerating edges were over five times more likely ($\chi^2_1 = 100.4$, $P < 0.001$) to be detected within the regenerating stand (183 of 218 observations, 84%) compared to the adjacent forest stand.

Stand age had a significant influence on space use between distance observations of 0–100 m and 101–200 m ($\chi^2_1 = 3.8$, $P = 0.050$) from the stand edge. Whip-poor-wills at regenerating edges had a greater probability ($\chi^2_1 = 26.6$, $P < 0.001$) of being detected within a distance of 0–100 m from the forest edge than a distance of 101–200 m from the nearest forest edge. Sixty-four percent (217 of 339) of observations occurred within 100 m of the forest edge. The distribution of Whip-poor-wills did not differ ($\chi^2_1 = 1.4$, $P = 0.76$) between 0–100 m and 101–200 m in forest areas. Fifty-four percent (86 of 157) of observations were recorded within a distance of 100 m from the stand edge.

The distribution of Whip-poor-wills within regenerating stands was highly skewed to forest edges. Whip-poor-wills within regenerating stands were more likely to be detected within 200 m of a forest edge than further away. This result was most pronounced in patches >20 ha where birds were more likely to be detected within 200 m of the forest edge compared to an expected random distribution among all available classes (all $\chi^2_3 = 91.6$, $P < 0.001$; $\chi^2_4 = 76.2$, $P < 0.001$; $\chi^2_5 = 79.9$, $P < 0.001$; and $\chi^2_5 = 85.8$, $P < 0.001$ for stands that were 21–30 ha, 31–40 ha, 41–50 ha, and > 50 ha, respectively) (Fig. 1). Detections within regenerating stands < 20 ha did not differ from random when compared

between 0–100 m and 101–200 m distance classes ($\chi^2_1 = 0.30$, $P = 0.58$). The shortest distance between opposing stand edges in patches < 20 ha was generally not > 400 m.

DISCUSSION

The presence of open regenerating stands had a positive effect on the density of Whip-poor-wills using this forested landscape. This suggests that regenerating stands provide some resource that Whip-poor-wills prefer for foraging or breeding. One possible explanation for high use of open habitats is that it provides greater access to prey. Both abundance and richness of adult lepidopteran insects, the primary food item of Whip-poor-wills (Cink 2002), can be influenced by timber management and have been shown to be greater in clear-cuts than forest interiors (Jokimaeki et al. 1998, Summerville and Crist 2002). Whip-poor-wills forage on aerial prey almost exclusively using a visual field with short, upward-directed flights initiated from on or near the ground. Foraging activity increases with lunar light intensity for this species (Mills 1986), possibly an adaptation for finding food by exploiting back-lit insects. Open habitats receive more lunar illumination and probably provide better opportunities for visual detection of prey. Regenerating stands may therefore provide both a richer prey base and better foraging conditions compared to mature forest stands with well-developed canopies.

Whip-poor-wills are ground nesters that require forested habitats (Bent 1940, Peck and James 1983, Cink 2002) with ground vegetation for nesting. The density of ground vegetation in our study area varied markedly between forest and regenerating patches. Forest patches contained dense, continuous thickets of ground-level vegetation and regenerating stands had sparse patchy ground vegetation.

Regenerating pine stands had a positive effect on use of adjacent mature stands by Whip-poor-wills. Responses to habitat adjacency often result from resource complementation when two adjacent patches contain distinctly different resources (Forman and Godron 1986, Dunning et al. 1992, Ries and Sisk 2004). This is consistent with the general belief that Whip-poor-wills require forested patches for nesting but use open areas including agricultural fields, scrub, and marshes for foraging (Cooper 1981, 1982; Alexander and Creswell 1990; Eastman 1991; Peterjohn and Rice 1991; Wang and Brigham 1997). Regenerating forests that are directly adjacent to mature stands may provide Whip-poor-wills the opportunity to exploit foraging and nesting habitats in close proximity.

The distribution of Whip-poor-wills near regenerating stands is consistent with a resource complementation argument. Whip-poor-will distribution within large regenerating stands was skewed to the edges that were adjacent to mature forest areas suggesting that territory placement was influenced by openings created by forest harvesting. This pattern would allow birds to effectively exploit resources from both habitat types. Observations of radio-tracked Whip-poor-wills from a separate study (Wilson 2003) support this suggestion. Males with both forested and regenerating habitats in close proximity typically roosted in forest habitat during the day, although they spent a disproportionately high amount of time foraging in regenerating stands at night.

The response of Whip-poor-wills to forest edges has direct implications for management of Whip-poor-will breeding populations in forested landscapes. Forest harvesting strategies that provide sustained yield of edge habitat by interspersing harvested patches with mid-rotation patches will favor Whip-poor-will populations. The amount of edge habitat available on a landscape scale is sensitive to both patch size and the level of interspersion between patch types (Franklin and Forman 1987). Management scenarios that use small to moderate patch sizes and spatially orchestrate harvests to maximize interspersion of patch types should be most useful.

ACKNOWLEDGMENTS

This study was funded through a cooperative agreement between Weyerhaeuser Company and the College of William and Mary. We thank M. A. Melchiors and D. A. Miller for the opportunities and administrative support to conduct the study, and Willam Barber and Kevin O'Kane for assistance in selecting study sites. We thank J. B. Cameron for field assistance. This manuscript was greatly improved after reviews by R. M. Brigham, C. P. Woods, and C. E. Braun. Finally, we are grateful to L. C. Whitaker, C. A. Adams, R. L. Peace, Anne Womack, G. D. Sciole, M. E. Roberts,

and C. A. Pope for administrative support from the College of William and Mary.

LITERATURE CITED

Alexander, I. and B. Cresswell. 1990. Foraging by Nightjars *Caprimulgus europaeus* away from their nesting areas. Ibis 4:568–574.

Bent, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. U.S. National Museum Bulletin 176.

Cink, C. L. 2002. Whip-poor-will (*Caprimulgus vociferous*). The birds of North America. Number 620.

Cooper, R. J. 1981. Relative abundance of Georgia caprimulgids based on call-counts. Wilson Bulletin 93:363–371.

Cooper, R. J. 1982. Range expansion of the Whip-poor-will in Georgia. The Oriole 47:1–9.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in boundary landscapes. Oikos 65:169–175.

Eastman, J. 1991. Whip-poor-will. Pages 252–253 *in* The atlas of breeding birds of Michigan (R. Brewer, G. A. McPeek, and R. J. Adams Jr., Editors). Michigan State University Press, East Lansing, USA.

Environmental Systems Research Institute (ESRI). 1992. ArcView 3.2. Environmental Systems Research Institute, Redlands, California, USA.

Forman, R. T. and M. Gordon. 1986. Landscape ecology. John Wiley and Sons, New York, USA.

Foster, J. and M. S. Gaines. 1991. The effects of a successional habitat mosaic on a small mammal community. Ecology 72:1358–1373.

Franklin, J. F. and R. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology 1: 5–18.

Hansson, L. 1977. Spatial dynamics of field voles, *Microtus agrestis*, in heterogeneous landscapes. Oikos 29:539–544.

Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The animal movement extension to Arcview. Version 2.0. USDI, Geological Survey, Alaska Science Center, Biological Science Office, Anchorage, USA.

Johnson, A. R., J. A. Wiens, B. T. Milne, and T. O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7:63–75.

Jokimaeki, J., E. Huhta, J. Itaemies, and R. Rahoko. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Canadian Journal of Forest Research 28:1068–1072.

Mills, A. M. 1986. The influence of moonlight on the behavior of goatsuckers. (Caprimulgidae). Auk 103:370–378.

Pearson, S. M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecology 3:13–18.

Peck, G. K. and R. D. James. 1983. Breeding birds of Ontario: nidiology and distribution. Volume 1. Non-passerines. Royal Ontario Museum of Life Sciences Miscellaneous Publication. Toronto, Ontario, Canada.

Peterjohn, B. G. and D. L. Rice. 1991. The Ohio breeding bird atlas. Ohio Department of Natural Resources, Columbus, USA.

Ries, L. and T. D. Sisk. 2004. A predictive model of edge effects. Ecology 85:2917–2926.

Rodewald, A. D. and R. H. Yahner. 2001. Influence of landscape composition on avian community structure and associated mechanisms. Ecology 82: 3493–3504.

Sisk, T. D., N. M. Haddad, and P. R. Ehrlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecological Applications 7:1170–1180.

Statsoft Inc. 1984–2005. Statistica (Data Analysis Software System). Version 6.1. Statsoft Inc., Tulsa, Oklahoma, USA.

Summerville, K. S. and T. O. Crist. 2002. Effects of timber harvest on forest lepidoptera: community, guild, and species responses. Ecological Applications 12:820–835.

Szaro, R. C. and M. D. Jackle. 1985. Avian use of a desert riparian island and its adjacent scrub habitat. Condor 87:511–519.

Thompson III, F. R., J. R. Probst, and M. G. Raphael. 1995. Impacts of silviculture: overview and management recommendations. Pages 201–219 *in* Ecology and management of neotropical migratory birds: a synthesis and review of critical issues (T. E. Martin and D. M. Finch, Editors). Oxford University Press, New York, USA.

Wang, K. and R. M. Brigham. 1997. Roost-site characteristics of Common Poorwills, *Phalaenoptilus nuttallii*, in Saskatchewan. Canadian Field-Naturalist 111:543–547.

Watts, B. D. 1996. Landscape configuration and diversity hotspots in wintering sparrows. Oecologia 108:512–517.

Wilson, M. D. 2003. Distribution, abundance, and home range of the Whip-poor-will (*Caprimulgus vociferous*) in a managed forest landscape. Thesis. College of William and Mary, Williamsburg, Virginia, USA.

Wilson, M. D. and B. D. Watts. 1999. Response of Brown-headed Nuthatches to thinning of pine plantations. Wilson Bulletin 111:56–60.

Wilson, M. D. and B. D. Watts. 2006. Effect of moonlight on detection of Whip-poor-wills: implications for long-term monitoring strategies. Journal of Field Ornithology 77:207–211.

The Wilson Journal of Ornithology 120(4):784–792, 2008

IMPACT OF HURRICANE WILMA ON MIGRATING BIRDS: THE CASE OF THE CHIMNEY SWIFT

MARK DIONNE,[1,2,3] CÉLINE MAURICE,[1] JEAN GAUTHIER,[1] AND FRANÇOIS SHAFFER[1]

ABSTRACT.—We documented the effects of hurricane Wilma (2005) on Chimney Swift (*Chaetura pelagica*) using data from the Québec Chimney Swift Survey Program and observations of swift mortality during migration. Hurricane Wilma developed in the Caribbean and followed the eastern coast of North America, moving over areas used extensively by migrating birds. Thousands of birds and, among them, Chimney Swifts, were caught and carried by the storm as far as Atlantic Canada and western Europe. At least 727 swifts were reported dead. Chimney Swift numbers in the province of Québec, Canada, declined significantly the following year, suggesting adverse consequences of the hurricane on this population over a large area. Roost counts declined by an average of 62%; the total Chimney Swift population decreased by approximately 50%. These results suggest that hurricanes can reduce the breeding population size of some migratory bird species. *Received 20 August 2007. Accepted 30 January 2008.*

There is increasing interest in the effect that extreme weather events can have on ecological processes and wildlife populations (Parmesan et al. 2000, Jentsch et al. 2007). Extreme weather conditions, including those caused by hurricanes, affect not only humans and their structures, but also wildlife by either altering or destroying important habitats (Wauer and Wunderle 1992) or by causing direct mortality (Dinsmore and Farnsworth 2006, Newton 2007). Migrating birds originating from eastern North America cross active hurricane paths and are at risk of encountering violent storms. Existing information on interactions between birds and hurricanes is rare and mostly anecdotal (Newton 2007). Typically, hurricanes, along the Atlantic coast of North America displace birds northward along the Atlantic coast or inland and are believed to kill some birds (Robertson and Muller 1961, Tuck 1968, Mills 1969, Anonymous 1998, Brinkley et al. 1997, Brinkley 1999, D'Anna 2004, Pulcinella and Lockyer 2004, NOAA 2005, Dinsmore and Farnsworth 2006).

Inclement weather conditions are known to cause significant mortality in birds. (Gessaman and Worthen 1982, Newton 2007). These events, when they occur during migration, can cause daily mortality rates much greater than the mean daily rate during nesting and wintering periods. The relative proportion of mortalities attributable to severe weather during migration is unknown and difficult to evaluate (Newton 2007). The effects of storms during migration are thought to be among possible factors affecting population levels of eastern North American songbirds (Butler 2000). Severe weather can also reduce numbers of some local breeding bird populations (Newton 2007). Understanding the adverse consequences of weather on birds is critical for declining species, species at risk, or species having low numbers and small, local distributions.

A record number of hurricanes occurred in the Atlantic Basin in 2005, causing considerable damage in many parts of eastern North America (NCDC 2006). We pursued two lines of evidence to examine the effect of hurricane activity on Chimney Swift (*Chaetura pelagica*) populations. First we summarized existing information on hurricane Wilma and Chimney Swift fallouts following this event to establish direct mortality associated with the hurricane. Second, we used data from a survey program established in 1998 by the Canadian Wildlife Service (CWS) to quantify the impacts of Wilma on Chimney Swift breeding population in Québec.

METHODS

Hurricane Wilma.—This hurricane coincided with migration of Chimney Swifts across

[1] Environment Canada, Canadian Wildlife Service, Québec Region, 1141 Route de l'Église, P. O. Box 10100, Québec, QC, G1V 4H5, Canada.

[2] Current address: 541, rue Jérôme Apartment 3, Québec, QC, G1K 5R5, Canada.

[3] Corresponding author; e-mail: calumix@hotmail.com

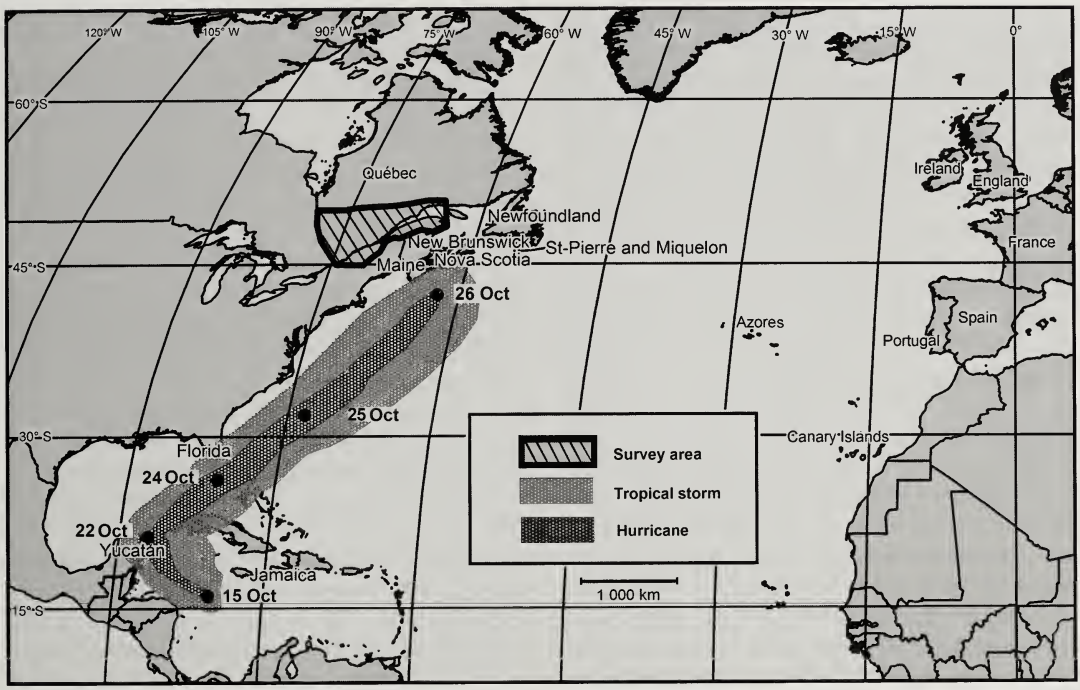


FIG.1. Trajectory and wind swaths of hurricane Wilma along the eastern Atlantic coast during October 2005 based on advisories 1 through 43 of the National Weather Service (National Hurricane Center) from the National Oceanographic and Atmospheric Administration. Black dots represent the position of the storm's eye. The figure was modified from: http://www.nhc.noaa.gov/archive/2005/WILMA_graphics.shtml. Position true at 30.00° N.

its path. Wilma began as a tropical depression on 15 October 2005 near Jamaica and moved towards the southwest, becoming a tropical storm on 17 October (Fig. 1; Pasch et al. 2006). The tropical storm proceeded in a west-north-west direction on 18 October, gaining strength and developing into a hurricane. Wilma became a category 5 hurricane (Saffir-Simpson Hurricane Scale) on 19 October with wind speeds increasing to 278 km/hr. Wind speeds peaked at 296 km/hr, while the estimated minimum central pressure intensity reached ~882 mb, a new record low for hurricanes in the Atlantic Basin. Hurricane Wilma lost strength and became a category 4 hurricane on 20 October with winds speeds reaching 241 km/hr. The eye's radius increased to 74 km and ranged between 74 and 111 km for most of the storm's lifetime. Wilma crossed and caused considerable damage to the northeastern Yucatán Peninsula on 22 October, emerging into the Gulf of Mexico on 23 October. After losing some vigor over land, the hurricane increased again in strength until it reached southern Florida, with winds reaching 194 km/hr (category 3 hurricane) on 24 October. Maximum winds decreased to 176 km/hr (category 2 hurricane) over Florida, causing extensive damage to the area. Wind speeds increased to 204 km/hr on 25 October. The hurricane lost strength on 26 October and became an extratropical cyclone with its eye ~370 km southeast of Halifax, Nova Scotia, Canada. The cyclone was then absorbed by another cyclone over eastern Nova Scotia on 27 October (Fig. 1; Pasch et al. 2006). Hurricane-force winds reached ~125 km in radius all through the storm, while tropical-force winds varied between 500 and 1,000 km in radius (Pasch et al. 2006).

Data Collection.—Hurricane data were obtained from the National Hurricane Center (NHC) of the United States' National Weather Service's website; the NHC is part of the National Oceanographic and Atmospheric Administration (NOAA). We collected observations of Chimney Swifts after hurricane Wilma from a variety of sources to document di-

rect hurricane-associated mortalities and sightings. All known birding and "newsgroup" websites were browsed for potential information on bird fallouts. Some sightings were validated by communicating directly with the originating persons. Concerned organizations in northeastern North America (U.S. Fish and Wildlife Service, university ornithology departments, birding associations and non-profit organizations providing care or rehabilitation services to injured birds) were contacted for information about unusual bird observations or mortalities after the passage of hurricane Wilma. Some birdwatchers reported unusual bird sightings directly to CWS.

We used data from the Chimney Swift Survey Program to quantify effects of the hurricane on Chimney Swift breeding populations. The Chimney Swift Survey Program was initiated in 1998 by CWS (Québec Region) to identify and characterize Chimney Swift roosting and nesting sites, and to monitor population trends. The study area covers the southern portion of the province; below the species' northern breeding range limit (Fig. 1). Over 331 different parishes were visited between 1998 and 2006 by volunteers (~100 people every year) and CWS employees. A parish is a religious territory, varying in both size and number of people. A small village usually has one parish while a town or a city may have two or more parishes. Every parish has a church, rectory, and school with old large masonry chimneys often used by Chimney Swifts. All potential Chimney Swift roosting and nesting sites in every parish were visited systematically starting in late May when swifts begin arriving from wintering areas. Roost surveys were conducted once or twice per week, throughout the breeding season and swifts were counted as they entered the roost. Monitoring started 30 min before sunset and lasted until birds were no longer visible. Surveys were conducted during clement weather (no rain and temperatures >15° C). The annual maximum number of birds seen at a given roost was compiled for two different time periods; at the beginning and the end of the breeding season. Spring counts conducted too close to the migration period were excluded because daily numbers can vary significantly and do not represent local swifts. Data from 1998 were not used because surveys effort was too low. Survey effort represents the number of roosts surveyed annually.

Statistical Analyses.—We calculated a "between-year change index" (BYCI): the maximum number of swifts recorded in year t + 1 divided by the number recorded at year t for each roost (Peach et al. 2004). Indices greater than one indicated an increase in swift numbers at a roost; those smaller than one, a decrease. Counts from a roost at the beginning and the end of the same breeding season were considered as distinct in the analysis, because birds adopt different flocking behavior after the breeding season and hatch-year birds may be present. Due to missing data, normality, and variance assumption violations, annual changes in Chimney Swift numbers at roosts were analyzed using a Friedman's test (nonparametric two-way ANOVA on ranked values). The 'between-year change index' (BYCI) was the response variable while 'roost' and 'period' were used as the explanatory categorical variables. Pairwise differences between 2005–2006 and other periods (1999–2000, 2000–2001, 2001–2002, 2002–2003, 2003–2004, 2004–2005) were tested using the least square means of ranked values. P-values for significant effects were adjusted using a layered Bonferroni correction to account for non-orthogonal multiple comparisons (Darlington 1990).

RESULTS

Bird Fallouts.—Unusual Chimney Swift sightings along the northeastern coast of North America began on 26 October, immediately after hurricane Wilma lost strength and became an extra-tropical cyclone. Birds were observed in many areas of northeastern North America at times when they are not usually present (Table 1). Thousands of Chimney Swifts were observed in Atlantic Canada (Nova Scotia, New Brunswick, Newfoundland), in Saint-Pierre and Miquelon (France), and in Maine (USA). Some notable bird counts per day (sum of the maximum count from different areas) were: 672 (Nova Scotia) and 325 (Saint-Pierre and Miquelon) on 27 October, 600 (New Brunswick) and 577 (Nova Scotia) on 28 October, thousands (Nova Scotia) on 30 October, more than 400 (Nova Scotia) on 31 October, 350 (Nova Scotia) on 1 November and ~2,000 (Maine) in

TABLE 1. Unusual Chimney Swift sightings in October-November 2005 following passage of hurricane Wilma based on web sites (azores.seawatching.net, birdingonthe.net, birdpac.org, birdsireland.com, surfbirds.com, ornithomedia.com, perso.orange.fr.), newsgroups (nf.birds, NatureNB, Nova Scotia Rare Birds Alerts), Alfrey 2005, Etcheberry 2005, Jiguet and Zucca 2005, SIGHS 2005, Dinsmore and Farnsworth 2006, and personal communications.

Location	October						November							
	26	27	28	29	30	31	1	2	3	4	5	6	7	10	11	?
New Brunswick, CA	10	125	600[b]	112		115[d]	125	1			15					
Nova Scotia, CA	101	672	577[b]		1,000's	>400	350		100's	2			70		3	
Newfoundland, CA		165	83	40[c]	3	1[a]	?		4							
Saint-Pierre and Miquelon, FR		325		108[a]												~2,000
Maine, USA												1[a]	1	1		
Azores Islands, PT			32	22	24	16	43	14	8	1						
Sein Island, FR					1		1									
Canary Island, ES				2												
England					2			3			1					
Ireland				4	3	3	4	2								

[a] found dead.
[b] 300 found dead in chimney.
[c] 17 found dead.
[d] 2 found dead.

TABLE 2. Annual results of the Quebec Chimney Swift Survey Program showing maximum bird counts and number of surveyed sites (effort), including nesting sites and roosts.

Year	# Birds	Surveyed sites
1999	3,568	58
2000	3,775	49
2001	2,197	36
2002	3,679	79
2003	4,044	52
2004	3,221	107
2005	4,847	183
2006	2,480	177

early November (Table 1). Chimney Swifts were also observed in areas of western Europe including the Azore Islands (Portugal), Canary Islands (Spain), and the Atlantic coasts of France, Ireland, and England (Table 1). Many observers also reported Chimney Swift mortalities: at least 727 were reported in northeastern North America (Table 1).

Chimney Swift Survey Program.—The total maximal annual count of Chimney Swifts in the province of Québec, Canada generally increased as new roosts were being discovered and monitoring efforts increased (Table 2). Survey efforts in 2005 were at their highest level and counts reached 4,847 birds. Total numbers of Chimney Swifts in 2006 declined by ~50% compared to 2005; survey efforts were similar and at their highest level during these 2 years. The Between-Year Change Index (BYCI) in Chimney Swift counts among roosts varied with time ($F = 4.52$; df = 6, 82; $P = 0.0005$). Chimney Swift numbers at roosts mostly increased prior to hurricane Wilma, but showed no consistent trend (Fig. 2). Unadjusted pairwise comparisons showed no significant difference in the periods prior to the hurricane, suggesting the mean number of Chimney Swifts/roost remained similar between 1999 and 2005. The BYCI subsequent to hurricane Wilma was significantly lower compared to previous periods, except 2000–2001 (Table 3). These results suggest a decrease in the mean number of Chimney Swifts/roost after hurricane Wilma. Roost numbers declined on average by 62% (Fig. 2) between 2005 and 2006.

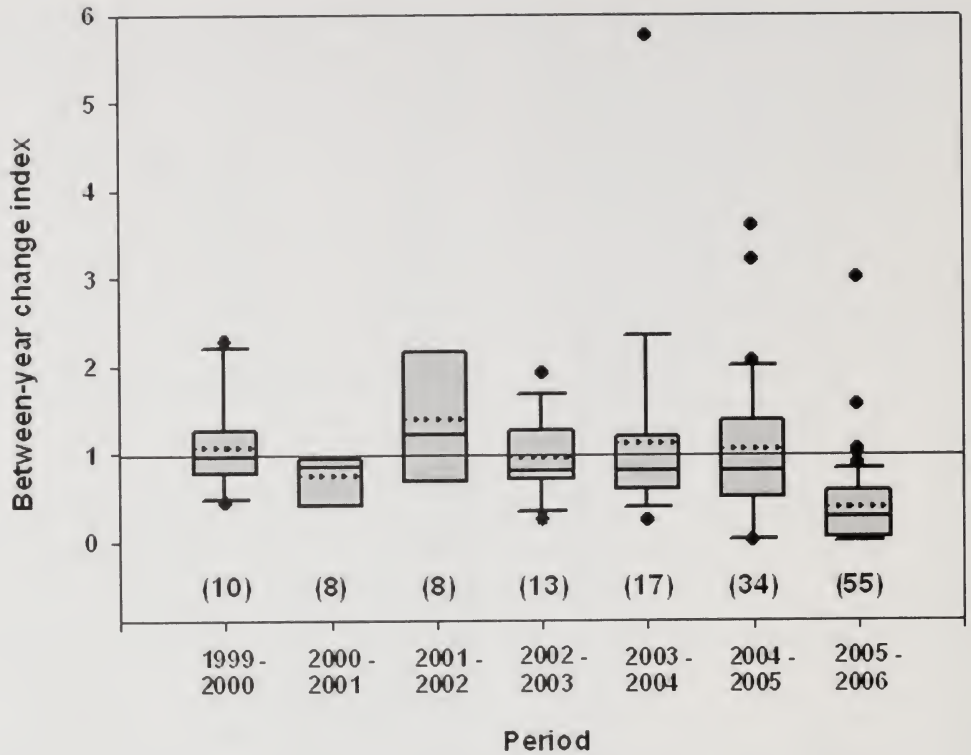


FIG. 2. Mean between-year index change in Chimney Swift numbers at known roosts in the province of Québec, Canada. The number of surveyed roosts for each period is indicated between parentheses under the plots. Dotted line represents the mean. The median corresponds to full line within the box's boundaries which represent the 25th and 75th percentiles. Whiskers represent the 10th and 90th percentiles, and outliers are indicated by dots.

DISCUSSION

Thousands of Chimney Swifts were observed in Atlantic Canada after passage of hurricane Wilma. Swifts are usually well on their way to wintering areas in South America at the time hurricane Wilma reached the Maritime Provinces. They normally leave this region to migrate at the end of August and, by September, most have left (Tuft 1986). Chimney Swifts depart northernmost range by September and southernmost range by mid- to late October (Kyle and Kyle 2005). This species can be observed during migration in the West Indies from August to October (Raffaele et al. 1998). Chimney Swifts are considered to be uncommon to fairly common autumn transients in the northeastern Yucatàn Peninsula from late August to early November (Howell and Webb 1995); the species is common on the Caribbean coasts of Costa Rica and Panama in October and November (Ridgely and Gwynne 1989, Stiles and Skutch 1989) and some have been reported as far as Peru in early November (Plenge et al. 1989). Late records of Chimney Swift sightings in northeastern North America have been scarce (Erskine 1992, David 1996). Reports from the Québec data base Étude des populations

TABLE 3. Between-year change index in roosts (least square means pairwise differences on ranked indices) between 2005–2006 and other periods in Quebec, Canada.

Period	Adjusted *P* value*
1999–2000	0.005
2000–2001	0.192
2001–2002	0.007
2002–2003	0.005
2003–2004	0.006
2004–2005	0.002

* *P* values were adjusted using the layered Bonferroni method.

d'oiseaux du Québec (ÉPOQ) show 1,649 Chimney Swift sightings in August, 239 in September, 14 in October, and none in November (Larivée 2007). ÉPOQ is a data set, which contains over 6 million bird reports made by birdwatchers year round in Québec. These include 11,968 sightings referring to Chimney Swifts between the end of April to 18 October from 1901 to 2006. No quantitative information is available for the Maritime Provinces, but Tuft (1986) mentions that swift sightings later than September are exceptional. Reverse migrations in the Maritime Provinces have, on occasion, been attributed to late summer dispersal and dawn reorientation towards the coast (Richardson 1982), but the fall event of 2005 strongly suggests that birds were carried off course by hurricane Wilma. This hypothesis is supported by the number of birds observed, timing of their arrival, and the condition in which many of them were found. A similar hurricane (Gladys) in 1968, in terms of intensity, timing, and route, carried Chimney Swifts as far as Nova Scotia (Mills 1969).

Birds displaced by hurricanes are probably either carried in the eye of the hurricane or blown by strong winds in the outer bands of the storm (Kaufman 1977). Many birds apparently become trapped in the eye of the hurricane, where the weather is calm, forcing them along the hurricane's path (Mills 1969, Jones 1999). There are several reports originating from hurricane hunter pilots (Philippsborn 1999, Halverson 2004), cargo ship passengers (Mayhew 1949, NOAA 2005) and inland hurricane witnesses (Theiss 2005, Dinsmore and Farnsworth 2006) of several birds being trapped inside the eye of a hurricane. The mechanisms by which birds become trapped inside a hurricane are not well understood. Most birds usually avoid storms and remain grounded until they pass (Sutton 1945, Richardson 1978, Butler 2000). These observations suggest that landbirds displaced by hurricanes are caught when flying over water where they cannot land nor find shelter (Newton 2007).

Chimney Swifts from northern and eastern areas of their breeding range converge during fall migration in the Mississippi Valley and, although some fly over Florida, most migrate across the Gulf of Mexico towards the Yucatàn Peninsula (Lowery 1943). We hypothesize that swifts displaced by hurricane Wilma were caught while crossing the Gulf of Mexico. This explanation is not entirely satisfactory, however, because birds could have landed and sought shelter when the eye of the hurricane passed over southern Florida. Swifts could also have been caught over land either blown by the powerful winds from rain bands around the storm's center or driven towards the center by the air flowing near the surface and converging in the storm's eye. We suspect that most displaced birds were caught on the Yucatàn Peninsula and over the Gulf of Mexico. Reports of thousands of Chimney Swifts in the storm's eye as it passed over Martin County, Florida on 24 October (Dinsmore and Farnsworth 2006) lend further weight to this hypothesis.

We believe that hurricane Wilma caused massive mortality of Chimney Swifts. When land birds are caught in hurricanes, some probably remain in constant flight during the storm's course and may be unable to feed during this time. When birds escaped the storm in Atlantic Canada, many were probably in poor physical condition. This suggests that many birds were unable to restore their body condition to resume migration and eventually died of starvation. Average temperature in Nova Scotia (Halifax) from 26 October to 11 November 2005 was 6.7 ± 3.1° C (Environment Canada 2007), making flying insects scarce and thermoregulation cost high. Two Chimney Swifts found dead on Grand Manan (New Brunswick) had lost between 30 and 35% of their average normal body weight (Brian Dalzell, Fundy Bird Observatory, pers. comm.). Starvation experiments revealed that adult Common Swifts (*Apus apus*) usually die when their weight decreases by 30% or more (Koskomies 1950). Many Chimney Swifts were reported to be in an advanced state of exhaustion (Kyle and Kyle 2006). The total number of deaths is probably largely underestimated, as many birds may have perished at sea. Numerous Chimney Swifts also died indirectly from the hurricane as a result of seeking shelter in active chimneys. Three hundred Chimney Swifts were found dead inside a chimney in use in Charlotte, New Brunswick on 28 October 2005 (Daniel Busby, CWS, pers. comm.).

The results from the Québec Chimney

Swift Survey Program suggest that hurricane Wilma reduced breeding populations of Chimney Swifts by as much as 50% over a large area. The Breeding Bird Survey (BBS) results also suggest a strong population decline for Canada between 2005 and 2006 with an annual index 50% lower in 2006 than in 2005 (Downes and Collins 2007). Other BBS results suggest that declines may have extended beyond Canada, into northeastern United States (Sauer et al. 2007). Data from the Québec Chimney Swift Program agree with existing information that suggests adverse weather during migration can cause decreases between 25 and 90% in breeding bird population numbers the following year (Newton 2007). Most studies, however, relate to smaller, local bird populations, which experience only temporary declines (Newton 2007). The survey area is large for the Québec Chimney Swift breeding population, covering ~200,000 km^2 (Fig. 1). Hurricane Wilma may possibly exacerbate the decline of Chimney Swifts. The BBS results indicate that Chimney Swifts have been declining in North America since 1966 (Sauer et al. 2007) and in Québec since 1968 (Downes and Collins 2007). The Canadian breeding Chimney Swift population is estimated at 10,000 breeding birds with 2,500 in Québec (Gauthier et al. 2007). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has recommended granting the status of 'threatened' to the species (COSEWIC 2007). Hurricanes could potentially accelerate declines of species such as Chimney Swift. Long term monitoring is necessary to learn if breeding numbers of Chimney Swift will recover from the effects of hurricane Wilma.

Our results demonstrate that hurricanes during migration can significantly impact breeding populations of some landbirds over wide areas. However, more typical hurricanes and severe storms may also affect population levels of some eastern songbirds (Butler 2000). Factors such as intensity, trajectory, frequency, and timing of storms and hurricanes are likely important in affecting birds. Extreme weather conditions including those caused by hurricanes could increase in frequency with climate change (Parry et al. 2007), potentially affecting more birds during migration. Further research is needed to identify species at most risk of suffering from severe weather conditions during migration, and to understand why and how birds get trapped by hurricanes. A continental network of observers is also necessary to standardize information on bird fallouts to increase the analytical power of acquired data and detecting actual impacts of hurricanes on different bird species.

ACKNOWLEDGMENTS

The authors thank all volunteer observers from the Québec Chimney Swift Survey Program, including Regroupement QuébecOiseaux, and Québec's ministère des Ressources naturelles et de la Faune, which provided reliable data on the species. We also thank J.-P. L. Savard, Pierre Laporte, and Mélanie Cousineau for constructive comments on this manuscript, as well as Michel Melançon for help on GIS mapping. We are grateful to all the birdwatchers who reported their valuable observations. Funding for this project was provided by the Canadian Wildlife Service, Québec Region (Environment Canada).

LITERATURE CITED

ALFREY, P. 2005. American vagrants on the Island of Corvo, Azores, in October 2005. Birding World 18:465–474.

ANONYMOUS. 1998. Hurricane Bonnie on Sable Island, Nova Scotia. Birders Journal 7:254.

BRINKLEY, E. S. 1999. The changing seasons: low pressure. North American Birds 53:12–19.

BRINKLEY, E. S., T. HASS, AND J. LOCKYER. 1997. The storms of 96′, Part 1: the storms and their associated birds. Audubon Society Field Notes 51: 819–829.

BUTLER, R. W. 2000. Stormy seas for some North American songbirds: are declines related to severe storms during migration? Auk 117:518–522.

COSEWIC. 2007. COSEWIC report on the status of the Chimney Swift (*Chaetura pelagica*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada.

D'ANNA, W. 2004. Hurricane Isabel (September 2003) in New York. Kingbird 54:14–19.

DARLINGTON, R. B. 1990. Regression and linear models. McGraw-Hill, New York, USA.

DAVID, N. 1996. Liste commentée des oiseaux du Québec. Association québécoise des groupes d'ornithologues, Montréal, Québec, Canada.

DINSMORE, S. J. AND A. FARNSWORTH. 2006. The changing season: weatherbirds. North American Birds 60:14–26.

DOWNES, C. M. AND B. T. COLLINS. 2007. Canadian bird trends web site. Version 2.2. Canadian Wildlife Service, Environment Canada, Gatineau, Québec, Canada.

ENVIRONMENT CANADA. 2007. Online historical daily temperatures from 26 October to 11 November 2005 for Halifax International Airport (Nova Scotia).

http://climate.weatheroffice.ec.gc.ca/climateData/almanac_e.html (accessed 13 December 2007).

Erskine, A. J. 1992. Atlas of breeding birds of the Maritime Provinces. Nimbus Publication Ltd. and Nova Scotia Museum, Halifax, Nova Scotia, Canada.

Etcheberry, R. 2005. The Wilma bird fallout, late October 2005 in Saint-Pierre et Miquelon. http://grandcolombier.com/geographie/nature/pdf-nature/fall_migration_2005_Wilmas_bird.pdf (accessed 13 December 2007).

Gauthier, J., M. Dionne, C. Maurice, J. Potvin, M. Cadman, and D. Busby. 2007. Status of the Chimney Swift (*Chaetura pelagica*) in Canada. Technical Report Series Number 477. Canadian Wildlife Service, Environment Canada, Québec City, Québec, Canada.

Gessaman, J. A. and G. L. Worthen. 1982. The effect of weather on avian mortality. Utah State Printing Services, Logan, Utah, USA.

Halverson, J. 2004. The eyes of hurricane Isabel. Weatherwise, January/February 2004, Washington, D.C., USA.

Howell, S. N. G. and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press, New York, USA.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and the Environment 5:365–374.

Jiguet, F. and M. Zucca. 2005. Report on a birdwatching trip to the Azores, 25 Oct–4 Nov 2005. http://azores.seawatching.net/reports/azores_2005_fjmz.pdf (accessed 13 December 2007).

Jones, R. M. 1999. Seabirds carried inland by tropical storm Nora. Western Birds 30:185–192.

Kaufman, K. 1977. The changing seasons: an intimate look at Kathleex and Oilier avian phenomena of autumn, 1976. American Birds 31:142–152.

Koskomies, J. 1950. The life of the swift, *Micropus apus* (L.), in relation to weather. Annales Academiae Scientiarum Fennicae, Series A 4:1–151.

Kyle, P. D. and G. Z. Kyle. 2005. America's mysterious birds above the fireplace. Texas A&M University Press, College Station, USA.

Kyle, P. D. and G. Z. Kyle. 2006. Avian aftermath of the 2005 hurricanes. Chaetura 11:12–13.

Larivée, J. 2007. Étude des populations d'oiseaux du Québec (ÉPOQ). Ornithological data base, Regroupement QuébecOiseaux, Rimouski, Québec, Canada.

Lowery Jr., G. H. 1943. The dispersal of 21,414 Chimney Swifts banded at Baton Rouge, Louisiana, with notes on probable migration routes. Proceedings of the Louisiana Academy of Science 7: 56–74.

Mayhew, J. R. 1949. Atmospheric pressure and bird flight. Science 109:403.

Mills, E. L. 1969. Hurricane "Gladys" and its ornithological effect on the Maritimes provinces. Nova Scotia Bird Society Newsletter 11:6–16.

NCDC. 2006. Climate of 2005, Atlantic hurricane season. National Climatic Data Center. http://www.ncdc.noaa.gov/oa/climate/research/2005/hurricanes05.html (accessed 21 August 2006).

Newton, I. 2007. Weather-related mass-mortality events in migrants. Ibis 149:453–467.

NOAA. 2005. National Oceanographic and Atmospheric Administration. http://www.srh.noaa.gov/jetstream/tropics/tc_structure.htm (accessed 19 October 2005).

Parmesan, C., T. L. Root, and M. R. Willig. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81:443–450.

Parry, M. L., O. F. Canziani, J. P. Palutikof, and co-authors. 2007. Technical Summary. Pages 23–78 *in* Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson, Editors). Cambridge University Press, Cambridge, United Kingdom.

Pasch, R. J., E. S. Blake, H. D. Cobb III, and D. P. Roberts. 2006. Tropical cyclone report, hurricane Wilma 15–25 October 2005. National Hurricane Center. http://www.nhc.noaa.gov/pdf/TCR-AL252005_Wilma.pdf (accessed January 28 2008).

Peach, W. J., S. R. Baillie, and S. T. Buckland. 2004. Current practices in the British Trust for Ornithology constant effort site scheme and comparisons of temporal changes in mist-net captures with changes in spot-mapping counts at the extensive scale. Studies in Avian Biology 29:46–56.

Philippsborn, R. 1999. Perspective from a NOAA hurricane hunter. NOAA News Online Story Number 272. National Oceanographic and Atmospheric Administration. http://www.noaanews.noaa.gov/stories/s272.htm (accessed 13 December 2007).

Plenge, M. A., T. A. Parker III, R. A. Hughes, and J. P. O'Neill. 1989. Additional notes on the distribution of birds in west-central Peru. Le Gerfaut 79:55–68.

Pulcinella, N. and J. Lockyer. 2004. Hurricane Isabel's birds with notes on previous tropical storms and storm related birds. Pennsylvania Birds 17:1–33.

Raffaele, H., J. Wiley, O. Garrido, A. Keith, and J. Raffaele. 1998. A guide to the birds of the West Indies. Princeton University Press, Princeton, New Jersey, USA.

Richardson, J. W. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

Richardson, J. W. 1982. Northeastward reverse migration of birds in Nova Scotia, Canada, in autumn - a radar study. Behavioral Ecology and Sociobiology 10:193–206.

Ridgely, R. S. and J. A. Gwynne Jr. 1989. A guide to the birds of Panama with Costa Rica, Nicaragua

and Honduras. Second Edition. Princeton University Press, Princeton, New Jersey, USA.

Robertson Jr., W. B., and H. B. Muller. 1961. Wild winds and wildlife. Audubon Magazine 63:308–311.

Sauer, J. R., J. E. Hines, I. Thomas, and J. Fallon. 2007. The North American Breeding Bird Survey, results and analysis 1966–2006. Version 10.13.2007, USGS, Patuxtent Wildlife Research Center, Laurel, Maryland, USA.

SIGHS. 2005. Wilma birds on Sable Island, October 2005. Sable Island Green Horse Society, Nova Scotia, Canada. http://www.greenhorsesociety.com/Birds%20-%20Wilma/Birds%20from%20Hurricane%20Wilma.htm (accessed 13 December 2007).

Stiles, F. G. and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

Sutton, G. M. 1945. Behavior of birds during a Florida hurricane. Auk 62:603–606.

Theiss, M. 2005. Hurricane Rita chase account. http://www.mthurricane.com/Hurricane_Rita.htm (accessed 13 December 2007).

Tuck, L. M. 1968. Recent Newfoundland bird records. Auk 85:304–311.

Tuft, R. W. 1986. Birds of Nova Scotia. Third Edition. Nimbus Publishing and the Nova Scotia Museum, Halifax, Canada.

Wauer, R. H. and J. M. Wunderle Jr. 1992. The effect of hurricane Hugo on bird populations on St. Croix, U.S. Virgin Islands. Wilson Bulletin 104:656–673.

The Wilson Journal of Ornithology 120(4):793–800, 2008

RED-COCKADED WOODPECKER HOME RANGE USE AND MACROHABITAT SELECTION IN A LOBLOLLY-SHORTLEAF PINE FOREST

DOUGLAS R. WOOD,[1,2,4] FRANCISCO J. VILELLA,[3] AND L. WESLEY BURGER JR.[1]

ABSTRACT.—We examined annual and seasonal home ranges of 41 Red-cockaded Woodpecker (*Picoides borealis*) groups from 1997 to 1999 in a Mississippi loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pine forest. Adaptive kernel annual home-range estimates ($\bar{x}$ = 43.1 ± 6.3 ha) were more conservative than maximum convex polygon estimates ($\bar{x}$ = 58.4 ± 4.5 ha). Mean non-nesting season home ranges were 15–20 ha greater than nesting season home ranges. Home ranges were smaller during nesting and increased during the post-fledging period. Compositional analysis revealed that Red-cockaded Woodpeckers selected habitats disproportionate to their availability annually and seasonally. Red-cockaded Woodpeckers selected pine sawtimber, pine poletimber, pine regeneration, and hardwood sawtimber habitats in that order. Home range appears to be a factor of landscape composition and inversely related to habitat quality. *Received 28 June 2004. Accepted 30 January 2008.*

The Red-cockaded Woodpecker (*Picoides borealis*) is an endangered species endemic to pine ecosystems in the southeastern United States (Jackson 1994). Red-cockaded Woodpeckers excavate cavities in old, live pines (*Pinus* spp.) and home ranges generally include a component of older pine stands (Jackson et al. 1979, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Conner et al. 1994). They prefer foraging stands with large, old (>60 yrs) pines and a limited hardwood component (Hooper and Harlow 1986, Jones and Hunt 1996, Zwicker and Walters 1999). Davenport et al. (2000) demonstrated a relationship in North Carolina between reproductive success and habitat quality. Group fitness was related to the number of cavities, limited under-story vegetation, and large diameter pine trees in the canopy. Similarly, Walters et al. (2002) reported that Red-cockaded Woodpecker fitness was related to moderate densities of large diameter pines, herbaceous ground cover, and removal of mid-story. This species serves as an indicator species for mature pine ecosystems of the southeastern United States (Jackson 1971, Escano 1995).

Studies throughout the species geographic range demonstrate extensive variation in mean home range size (14–225 ha; Table 1). Doster and James (1998) calculated a range-wide mean of 76.1 ha from published studies. Red-cockaded Woodpeckers also exhibit seasonal shifts in home range. Jerauld et al. (1983) reported that woodpeckers constricted their home ranges by 40–60% during nesting. Conversely, home ranges may be substantially expanded during the non-nesting season; Skorupa and McFarlane (1976) reported they doubled their home range size during the non-nesting season. Habitat loss or habitat quality may influence home range size (Nesbitt et al. 1983, Jackson and Parris 1995, Doster and James 1998).

Previous studies of Red-cockaded Woodpecker home ranges used different field methods, which makes comparisons among studies difficult. Timing of observations (seasonal or annual), small numbers of groups observed/year, duration of observations, and time between locations all varied among home range studies. For example, several studies used a diel (dawn-dusk) approach (Sherrill and Case 1980, DeLotelle et al. 1995), whereas others used observation periods of 2–14 hrs (Hooper et al. 1982, Hardesty et al. 1997, Doster and James 1998). Similarly, several studies used hourly locations (Hooper et al. 1982), whereas others used locations recorded in 5-min intervals (DeLotelle et al. 1987).

Different methods have also been used to

[1] Box 9690, Department of Wildlife and Fisheries, Mississippi State, MS 39762, USA.

[2] Current address: PMB 4068, Southeastern Oklahoma State University, 1405 North 4th Avenue, Durant, OK 74701, USA.

[3] Box 9691, Mississippi Cooperative Fish and Wildlife Research Unit, Mississippi State, MS 39762, USA.

[4] Corresponding author: e-mail: dwood@se.edu

TABLE 1. Home range studies throughout the geographic range of the Red-cockaded Woodpecker.

Study	State	Season	Forest type	# groups	$\bar{x}$ (ha)
Bradshaw (1995)	VA	Annual	Loblolly	6	91.3
Crosby (1971)	FL	Nesting	Longleaf	2	17.2
DeLotelle et al. (1995)	FL	Annual	Longleaf	13	129
Doster and James (1998)	AR	Annual	Shortleaf	5	24.8
Epting et al. (1995)	FL/GA	Annual	Mixed	18	79.8
Hardesty et al. (1997)	FL	Annual	Longleaf	20	108.8
Hooper et al. (1982)	SC	Annual	Mixed	24	86.9
Jackson and Parris (1995)	LA	Annual	Mixed	8	135
Nesbitt et al. (1978)	FL	Non-nesting	Mixed	3	69.8
Sherrill and Case (1980)	SC	Non-nesting	Longleaf	4	32.1
Skorupa and McFarlane (1976)	SC	Annual	Mixed	2	41.9
Wood (1983)	OK	Nesting	Slash	1	44.1
Wood et al. (this study)	MS	Annual	Loblolly	41	58.4

calculate home ranges including minimum convex polygon (Sherrill and Case 1980, DeLotelle et al. 1995), maximum convex polygon (Hooper et al. 1982, Jackson and Parris 1995), and adaptive kernel (Hardesty et al. 1997). Each estimation method has advantages and disadvantages. Minimum or maximum convex polygon methods often inflate home range estimates by including areas not actually used by woodpeckers. Conversely, adaptive kernel methods incorporate repeated locations and actual use of inclusive habitat types, which may provide more conservative estimates of home range.

Animals exhibit habitat selection at multiple spatial scales and may use different proximate cues at different spatial scales (Johnson 1980, Orians and Whittenberger 1991). Most woodpecker habitat selection studies focus on microhabitat selection because woodpeckers typically occur in relatively homogenous mature pine stands (Jones and Hunt 1996, Zwicker and Walters 1999). However, some studies have examined within-stand type and age-class selection by Red-cockaded Woodpeckers. Hooper and Harlow (1986) in South Carolina and Jones and Hunt (1996) in Louisiana found that woodpeckers selected pine stands >30 years of age, but avoided pine stands <30 years of age and mature hardwood stands. Many populations of woodpeckers occur in relatively homogenous landscapes, but others occur in highly fragmented landscapes which provide an opportunity to examine macrohabitat selection in heterogeneous loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pine forests (USDI 2003).

Our objectives were to: (1) estimate Red-cockaded Woodpecker home ranges at three temporal scales (annual, nesting, and non-nesting seasons) in a loblolly-shortleaf pine forest, (2) estimate home range size for a large number ($\geq$12) of groups annually, (3) calculate home ranges using adaptive kernel and maximum convex polygon methods for comparison with other studies, and (4) examine macrohabitat selection within home ranges using compositional analysis.

METHODS

Study Area.—The Bienville National Forest in central Mississippi is 72,216 ha of pine, pine-hardwood, and hardwood stands of differing age classes in a fragmented landscape. Dominant tree species include loblolly and shortleaf pine intermixed with low densities of longleaf pine (*Pinus palustris*), slash pine (*P. ellioti*), oak (*Quercus* spp.), hickory (*Carya* spp.), and sweetgum (*Liquidambar styraciflua*) (Wood 2001).

Field Procedures.—We randomly selected, without replacement, a subsample of 15 Red-cockaded Woodpecker groups/year for visual observation from the 104–106 groups at the study site. However, due to the dynamic nature of Red-cockaded Woodpecker groups (e.g., groups disband due to predation or dispersal), some groups were omitted during the course of the study. We observed 41 different groups (1997, n = 15; 1998, n = 14; 1999, n

= 12) at Bienville National Forest. We banded 115 adult and 54 nestlings to identify individuals in each group (Wood et al. 2001); this represents 70% of the individuals in our study groups.

We conducted ~1,925 hrs of observations from 1997 to 1999 on 41 groups ($\bar{x}$ = 47 observation hrs/group). Five-hour visual observation periods were performed on each group for 1 year beginning in January and concluding in December. Observation periods were performed sequentially by group throughout the year to approximate equal effort, and each group was followed at least once per month. Each observation period began at first light and contact was maintained for 5 hours (Hooper and Harlow 1986, Engstrom and Sanders 1997). Each observation period was divided into 6-min periods consisting of a 1-min visual observation period followed by a 5-min waiting period when no data were collected (Sherrill and Case 1980, Hooper et al. 1982, DeLotelle et al. 1983). Frequent observation periods enabled us to detect rapid changes in habitat use in the fragmented landscape of Bienville National Forest. One woodpecker was selected at the beginning of the 1-min observation period; all locations of that bird were marked with flagging and subsequently georeferenced with a differentially-corrected Global Positioning System unit. Red-cockaded Woodpeckers typically forage in proximity and the whole group can not be observed simultaneously; we believe that selecting an individual from the group was representative of the groups' location at any given time period. We defined the group as the sampling unit for home-range analysis and pooled all locations from all individuals in each group observed during the visual observation periods.

Statistical Analyses.—We used the animal movement extension in ArcView version 3.2 to estimate annual (1 Jan–1 Dec), non-nesting (1 Jan–31 Mar and 1 Aug–31 Dec), and nesting (1 Apr–31 Jul) season home ranges. We calculated 100% maximum convex polygon (MCP) home ranges and 95% adaptive kernel home ranges. Kernel methods account for repeated locations whereas MCP methods do not (Seaman and Powell 1996, Seaman et al. 1999). Adaptive kernel methods are better suited for analysis of location data collected in a truncated manner (e.g., 5-hr visual observation periods; Swihart and Slade 1985). However, adaptive kernel methods may underestimate home ranges of species that have a defended resource centrally located in their territory (Worton 1989). A balanced ANOVA model with group as a random effect (SAS 1985) was used to test for differences in annual, non-nesting, and nesting season home ranges.

We used compositional analysis to test for differences between habitat use and availability within annual, non-nesting, and nesting season home ranges (Aebischer et al. 1993). Habitat types within home ranges were defined as those habitats and age classes available at Bienville National Forest. Habitat types included pine regeneration (0–20 yrs), pine poletimber (21–50 yrs), pine sawtimber (51–110 yrs), and hardwood sawtimber (51–100 yrs). Woodpecker locations were assigned to habitat type using points derived by GPS locations collected in the field. Locations were imported into ArcView and combined with a map layer of habitat types to identify which locations occurred in different habitat types. We summed the proportion of locations for each habitat to 1.0 for compositional analysis.

Spatial Analyst in ArcView was used to calculate the proportion of locations available for each habitat type. Compositional analysis was performed using the program RESOURCE SELECTION for Windows 1.00b8.4© (Leban 1999). Compositional analysis uses a MANOVA on differences in the log ratios of use and availability proportions to test for a main effect (Aitchison 1986). Habitat use and availability proportions are log-ratio transformed which makes the observations linearly independent (Aitchison 1986). Compositional analysis uses a generalized likelihood ratio statistic to calculate an overall Chi-square test statistic. Pair-wise comparisons were used, if a main effect was detected, to test and rank habitat preferences. All statistical tests were evaluated for significance at $\alpha = 0.05$; home range means ± SE are presented.

RESULTS

Home Range.—MCP home-range estimates were generally greater than adaptive kernel estimates, although not for the nesting season (Table 2). Both methods detected similar differences between annual and seasonal home-

TABLE 2. Maximum convex polygon (MCP) and adaptive kernel (AK) methods for calculating Red-cockaded Woodpecker annual, non-nesting, and nesting season home ranges (ha) at Bienville National Forest, Mississippi, 1997–1999.

Method	Season	$\bar{x}$	SE	Range
MCP	Annual	58.4	4.5	14.4–201.5
	Non-nesting	43.7	3.5	9.8–122.0
	Nesting	24.1	2.2	5.6–66.0
AK	Annual	43.1	6.3	3.6–252.8
	Non-nesting	39.1	2.7	10.0–79.4
	Nesting	24.4	5.2	1.0–214.9

range sizes. Annual home ranges ($\bar{x}$ = 58.4 ± 4.5 ha) using 100% MCP home ranges were larger than nesting season home ranges ($\bar{x}$ = 24.1 ± 2.2 ha; $F_{1,39}$ = 51.5, P = 0.047). However, annual home ranges were not larger than non-nesting season home ranges ($\bar{x}$ = 43.7 ± 3.5 ha, $F_{1,39}$ = 29.2, P = 0.15). Red-cockaded Woodpeckers increased their non-nesting season home-range size by ~20 ha compared to average nesting season home ranges ($F_{1,39}$ = 2147.3, P = 0.02).

Adaptive kernel estimates of annual home ranges ($\bar{x}$ = 43.1 ± 6.3 ha) were larger than nesting season ($\bar{x}$ = 24.4 ± 5.2 ha) home ranges ($F_{1,39}$ = 28.47, P = 0.04), but were not larger than non-nesting season home ranges ($\bar{x}$ = 39.1 ± 2.7 ha; $F_{1,39}$ = 2.40, P = 0.34). Red-cockaded Woodpeckers increased their non-nesting season home ranges by ~15 ha compared with the average nesting season home range ($F_{1,39}$ = 599.7, P = 0.03).

The sum of the nesting and non-nesting season home ranges with both methods often exceeded annual home-range size. Examination of ArcView products of individual home ranges showed that woodpeckers used core areas near the cavity trees in all seasons, but frequently incorporated habitat patches outside the nesting season home range during the non-nesting season. This produced annual home range estimates larger than either seasonal home range estimate for some woodpecker groups.

Macrohabitat Selection.—Red-cockaded Woodpeckers selected habitats disproportionate to their availability annually (χ^2_3 = 27.0, $P < 0.001$) and during the nesting (χ^2_3 = 12.4, P = 0.001) and non-nesting (χ^2_3 = 21.0, $P < 0.001$) seasons (Table 3). Woodpeckers selected (1) pine sawtimber, (2) pine poletimber, (3) pine regeneration, and (4) hardwood sawtimber in that order. Regardless of season, pair-wise comparisons indicated that woodpeckers disproportionately selected pine sawtimber over the other habitat types. No differences were detected for habitat selection among pine poletimber, pine regeneration, and hardwood sawtimber.

DISCUSSION

Home Range.—Both adaptive kernel ($\bar{x}$ = 43.1 ha) and MCP ($\bar{x}$ = 58.4 ha) estimates of Red-cockaded Woodpecker home ranges at Bienville National Forest were smaller than the 76.1 ha range-wide estimate calculated by Doster and James (1998). MCP methods provided a realistic estimate of the furthest extent of Red-cockaded Woodpecker activity. How-

TABLE 3. Red-cockaded Woodpecker annual and seasonal habitat use and availability at Bienville National Forest, Mississippi, 1997–1999.

Season	Habitat type	% Use (range)	% Availability (range)
Annual	Pine sawtimber	87 (18–100)	74 (28–100)
	Pine poletimber	6 (0–77)	7 (0–31)
	Pine regeneration	5 (0–24)	14 (0–35)
	Hardwood sawtimber	2 (0–21)	5 (0–67)
Nesting	Pine sawtimber	88 (6–100)	82 (28–100)
	Pine poletimber	7 (0–90)	6 (0–63)
	Pine regeneration	4 (0–25)	11 (0–53)
	Hardwood sawtimber	1 (0–24)	1 (0–12)
Non-nesting	Pine sawtimber	83 (29–100)	77 (37–100)
	Pine poletimber	7 (0–61)	6 (0–38)
	Pine regeneration	6 (0–26)	14 (0–50)
	Hardwood sawtimber	4 (0–43)	3 (0–30)

ever, stands or areas are included in the home-range estimate that may not have been used by Red-cockaded Woodpeckers. Conversely, maximum convex polygon methods did not account for repeated uses of locations. Adaptive kernel methods more accurately reflected actual habitat use by Red-cockaded Woodpeckers and accounted for repeated locations. Adaptive kernel methods may be more accurate in estimating Red-cockaded Woodpecker home range and reflect a more conservative estimate of home range.

Mean Red-cockaded Woodpecker home-range size in the Bienville National Forest was similar to the mean breeding season home range (46.5 ha) in a Florida longleaf pine forest (DeLotelle and Epting 1992) and in southwest Georgia (47.1 ha) (Engstrom and Sanders 1997). However, mean home range at Bienville National Forest was greater than (24.8 ha) in an Arkansas shortleaf pine forest (Doster and James 1998), where habitat availability may have restricted Red-cockaded Woodpecker home-range size. Similarly, (Bradshaw 1995) attributed Red-cockaded Woodpecker home-range size in Virginia to the extent of isolation of mature loblolly pine stands compared to the surrounding landscape matrix of pine plantations and agricultural areas.

Hooper et al. (1982) reported a mean Red-cockaded Woodpecker home range of 87 ha in a South Carolina longleaf pine forest using the maximum convex polygon method, approximately twice the mean home range at Bienville National Forest, but with a similar range (34–225 ha) to those at Bienville National Forest. Hardesty et al. (1997) conducted a similar study in longleaf pine forests at Eglin Air Force Base in Florida using adaptive kernel methods and documented a mean home range of 108.8 ha (range = 64–387 ha).

Seasonal Home Range Shifts.—Red-cockaded Woodpeckers on average increased their non-nesting season home ranges by 15–20 ha: 85% (35/41) of Red-cockaded Woodpecker groups had larger non-nesting season than nesting season home ranges. Three of six groups that had larger nesting season than non-nesting season home ranges were in seed tree cuts (i.e., the cavity trees functioned as the seed trees in a pine regeneration stand) or were adjacent to young pine plantations. This frequently required woodpeckers to traverse longer distances to obtain prey, especially while feeding nestlings, than groups in mature pine stands (Wood 2001). One group shifted from their active cluster area to a recently abandoned cluster area to nest, yet returned to their active cavities for roosting during the nesting season inflating their apparent home-range size. Two other groups exhibited larger nesting season than non-nesting season home ranges. Both groups appeared to occupy high-quality habitat and there is no obvious explanation for the larger nesting season home range.

Red-cockaded Woodpeckers in a Virginia loblolly pine forest expanded their home ranges from 46 to 75 ha during the nesting season and from 84 to 167 ha during the non-nesting season (Bradshaw 1995). Similarly, in a South Carolina longleaf pine forest, Skorupa and McFarlane (1976) reported an increase of 72–113% in Red-cockaded Woodpecker home-range size during the non-nesting season. Conversely, Jerauld et al. (1983) reported that Red-cockaded Woodpeckers used only 36–47% of their annual home range during the nesting season. However, Hooper et al. (1982) documented larger home ranges during nesting than during the non-nesting season. Non-nesting home ranges were 21% smaller than nesting season home ranges.

Home Range and Habitat Quality.—An inverse relationship between habitat quality and home-range size has been documented for species including Belted Kingfisher (*Megaceryle alcyon*) (Davis 1982), Lapland Longspurs (*Calcarius lapponicus*) (Seastedt and MacLean 1979), and warblers (Parulinae) (Morse 1976). Does an inverse relationship between foraging quality and home-range size exist for Red-cockaded Woodpeckers? Theoretically, Red-cockaded Woodpecker groups in higher quality foraging habitat would have smaller home ranges than woodpecker groups in lower quality habitats (DeLotelle et al. 1987). Red-cockaded Woodpeckers with proximate access to suitable foraging habitat would expend less energy to obtain resources than those that must traverse or circumvent unsuitable habitats to meet the same energetic requirements (Doster and James 1998).

DeLotelle et al. (1987) reported greater Red-cockaded Woodpecker home-range size in a longleaf pine forest in Florida than home ranges in a longleaf pine forest in South Car-

olina which had better microhabitat quality. Epting et al. (1995) reported a mean home range of 67 ha in a mixed longleaf-loblolly pine forest at Fort Stewart in Georgia. Home ranges at Fort Stewart were correlated with habitat quality including increased pine basal area and decreased area of hardwood stands. Epting et al. (1995) compared the Fort Stewart population with one in longleaf pine in Florida that had a mean home range of 116 ha. They suggested that Red-cockaded Woodpeckers in Georgia had higher quality habitats than those in Florida.

Nesbitt et al. (1983) reported large nesting season home ranges (~144 ha) in Florida and speculated that large Red-cockaded Woodpecker home ranges were due to low habitat quality. However, Nesbitt et al. (1983) could not establish a significant relationship between habitat quality and home range. Hooper et al. (1982) reported a strong relationship between presence of suitable foraging habitat near the nest cluster and Red-cockaded Woodpecker home-range size. Generally, presence of hardwood stands or pine plantations may increase home-range size without contributing significantly to prey availability.

Macrohabitat Selection.—Compositional analysis at Bienville National Forest revealed that pine sawtimber stands were strongly preferred, even though pine sawtimber stands had high availability. This relationship may partially be a function of Red- cockaded Woodpecker groups within pine sawtimber stands and proximity to pine sawtimber stands managed intensively for Red-cockaded Woodpecker foraging habitat (USDA 1995). Most Red-cockaded Woodpecker nest clusters were surrounded by suitable patches of pine sawtimber, but several were adjacent to pine regeneration, pine poletimber, hardwood sawtimber stands, and agricultural areas. We frequently observed Red-cockaded Woodpeckers bypassing these less suitable stands to forage in 90–110 year old pine stands.

Pine poletimber was the second most frequently selected habitat annually and seasonally. However, pine poletimber stands were not used disproportionately to availability and were not considered suitable for cavity placement due to their young age (25–50 yrs of age) and high stocking densities (USDI 1985). However, pine poletimber can serve as suitable foraging habitat (Hooper and Harlow 1986, Wigley et al. 1999, Wood 2001).

Pine regeneration stands ranked third in order of habitat selection. Pine regeneration stands had a relatively high availability (11–14%, range = 0–53%), due primarily to intensive timber harvest and even-aged silvicultural methods (USDA 1995). However, Red-cockaded Woodpecker use (4–6%, range = 0–26%) of pine regeneration stands was regularly less than its availability. Red-cockaded Woodpeckers generally avoided pine regeneration stands, even when a group's cavities were within a pine regeneration stand. Specifically, in the mid-1980s, ~25 Red-cockaded Woodpecker cluster areas were regenerated as seed tree cuts with active Red-cockaded Woodpecker cavity trees left as the seed trees. These woodpeckers had to traverse open areas to access foraging sites. Red-cockaded Woodpeckers used pine regeneration stands at low rates, but many of the stems selected for foraging were large dbh seed trees within the regeneration stand. The mean dbh of stems selected for foraging in pine regeneration stands was 47 ± 15 cm (range = 7.5–79 cm; Wood 2001). Thus, many of the stems were large dbh pines; small dbh pines were rarely selected for foraging by Red-cockaded Woodpeckers (Zwicker and Walters 1999).

Hardwood sawtimber was the least preferred habitat type in the Bienville National Forest. Several hardwood sawtimber stands were proximally located to woodpecker groups and received high seasonal proportion of foraging by Red-cockaded Woodpeckers; however, large pine stems were overwhelmingly selected by Red-cockaded Woodpeckers (Wood et al. 2005). Due to overall low availability of hardwood sawtimber, pine poletimber, and pine regeneration, use and availability proportions may have exerted leverage on habitat selection models. Thus, the order of selection for habitat types with low availability and use may be a function of the sensitivity of the statistical models rather than biological selection by Red-cockaded Woodpeckers.

ACKNOWLEDGMENTS

We thank our field technicians for their dedicated work under difficult conditions. We thank M. C. Brittingham, R. N. Conner, K. G. Smith, H. D. Wilkins, and 2 anonymous reviewers for providing comments

on the manuscript. We are grateful to the U. S. Forest Service, National Council of the Paper Industry for Air and Stream Improvement, Forest and Wildlife Research Center at Mississippi State University, and the Mississippi Cooperative Fish and Wildlife Research Unit for financial support for this research. We thank the Mississippi Department of Wildlife, Fisheries, and Parks for logistical support.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313–1325.

Aitchison, J. 1986. The statistical analysis of compositional data. Chapman and Hall, London, United Kingdom.

Bradshaw, D. S. 1995. Habitat use by a relict population of Red-cockaded Woodpeckers in southeastern Virginia. Pages 482–488 *in* Red-cockaded Woodpecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Editors). Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin University, Nacodoches, Texas, USA.

Conner, R. N. and K. A. O'Halloran. 1987. Cavity-tree selection by Red-cockaded Woodpeckers as related to growth dynamics of southern pines. Wilson Bulletin 99:398–412.

Conner, R. N., D. C. Rudolph, D. Saenz, and R. R. Schaefer. 1994. Heartwood, sapwood, and fungal decay associated with Red-cockaded Woodpecker cavity trees. Journal of Wildlife Management 58: 728–734.

Crosby, G. T. 1971. Home range characteristics of the Red-cockaded Woodpecker in north-central Florida. Pages 60–73 *in* Ecology and management of the Red-cockaded Woodpecker (R. L. Thompson, Editor). USDI, Bureau of Sport Fisheries and Wildlife and Tall Timbers Research Station, Tallahassee, Florida, USA.

Davenport, D. E., R. A. Lancia, J. R. Walters, and P. D. Doerr. 2000. Red-cockaded woodpeckers: a relationship between reproductive fitness and habitat in the North Carolina sandhills. Wildlife Society Bulletin 28:426–434.

Davis, J. D. 1982. Territory size in *Megaceryle alcyon* along a stream habitat. Auk 99:353–362.

DeLotelle, R. S. and R. J. Epting. 1988. Selection of old trees for cavity excavation by Red-cockaded Woodpeckers. Wildlife Society Bulletin 16:48–52.

DeLotelle, R. S. and R. J. Epting. 1992. Reproduction of the Red-cockaded Woodpecker in central Florida. Wilson Bulletin 104:285–294.

DeLotelle, R. S., J. R. Newman, and A. E. Jerauld. 1983. Habitat use by Red-cockaded Woodpeckers in central Florida. Pages 59–67 *in* Red-cockaded Woodpecker Symposium II (D. A. Wood, Editor). Florida Game and Freshwater Fish Commission, Tallahassee, USA.

DeLotelle, R. S., R. J. Epting, and J. R. Newman. 1987. Habitat use and territory characteristics of Red-cockaded Woodpeckers in central Florida. Wilson Bulletin 99:202–217.

DeLotelle, R. S., R. J. Epting, and G. Demuth. 1995. A 12-year study of Red-cockaded Woodpeckers in central Florida. Pages 259–269 *in* Red-cockaded Woodpecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Editors). Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin University, Nacodoches, Texas, USA.

Doster, R. H. and D. A. James. 1998. Home range size and foraging habitat of Red-cockaded Woodpeckers in the Ouachita Mountains of Arkansas. Wilson Bulletin 110:110–117.

Engstrom, R. T. and F. J. Sanders. 1997. Red-cockaded Woodpecker foraging ecology in an old-growth longleaf pine forest. Wilson Bulletin 109: 203–217.

Epting, R. J., R. S. DeLotelle, and T. Beaty. 1995. Red-cockaded Woodpecker territory and habitat use in Georgia and Florida. Pages 270–276 *in* Red-cockaded Woodpecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Editors). Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin University, Nacodoches, Texas, USA.

Escano, R. E. F. 1995. Red-cockaded Woodpecker extinction or recovery: summary of status and management of our national forests. Pages 28–35 *in* Red-cockaded Woodpecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Editors). Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin University, Nacodoches, Texas, USA.

Hardesty, J. L., K. E. Lucas, and H. F. Percival. 1997. Ecological correlates of Red-cockaded Woodpecker (*Picoides borealis*) foraging preference, habitat use, and home range size in northwest Florida (Eglin Air Force Base). Final Report. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, USA.

Hooper, R. G. and R. F. Harlow. 1986. Forest stands selected by foraging Red-cockaded Woodpeckers. USDA, Forest Service, Research Paper SE–259. Asheville, North Carolina, USA.

Hooper, R. G., L. J. Niles, R. F. Harlow, and G. W. Wood. 1982. Home ranges of Red-cockaded Woodpeckers in coastal South Carolina. Auk 99: 675–682.

Jackson, J. A. 1971. The evolution, taxonomy, distribution, past populations, and current status of the Red-cockaded Woodpecker. Pages 4–29 *in* Ecology and management of the Red-cockaded Woodpecker (R. L. Thompson, Editor). USDI, Bureau of Sport Fisheries and Wildlife and Tall Timbers Research Station, Tallahassee, Florida, USA.

Jackson, J. A. 1994. Red-cockaded Woodpecker (*Picoides borealis*). The birds of North America. Number 85.

Jackson, J. A. and S. D. Parris. 1995. The ecology

of Red-cockaded Woodpeckers associated with construction and use of a multi-purpose range complex at Fort Polk, Louisiana. Pages 277–282 *in* Red-cockaded Woodpecker: recovery, ecology, and management (D. L. Kulhavy, R. G. Hooper, and R. Costa, Editors). Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin University, Nacodoches, Texas, USA.

Jackson, J. A., M. R. Lennartz, and R. G. Hooper. 1979. Tree age and cavity initiation by Red-cockaded Woodpeckers. Journal of Forestry 77:102–103.

Jerauld, A. E., R. S. DeLotelle, and J. R. Newman. 1983. Restricted Red-cockaded Woodpecker clan movement during reproduction. Pages 97–98 *in* Red-cockaded Woodpecker Symposium II (D. A. Wood, Editor). Florida Game and Freshwater Fish Commission, Tallahassee, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, C. M. and H. E. Hunt. 1996. Foraging habitat of the Red-cockaded Woodpecker on the D'Arbonne National Wildlife Refuge, Louisiana. Journal of Field Ornithology 67:511–518.

Leban, F. A. 1999. Resource selection for Windows: user's guide. F. A. Leban, University of Idaho. Moscow, USA.

Morse, D. H. 1976. Variables affecting the density and territory size of breeding spruce-woods warblers. Ecology 57:290–301.

Nesbitt, S. A., D. T. Gilbert, and D. B. Barbour. 1978. Red-cockaded Woodpecker fall movements in a Florida flatwoods community. Auk 95:145–151.

Nesbitt, S. A., B. A. Harris, A. E. Jerauld, P. J. Skoog, C. B. Brownsmith, and G. L. Evink. 1983. Response of a male Red-cockaded Woodpecker to drastic habitat alteration. Pages 101–104 *in* Red-cockaded Woodpecker Symposium II (D. A. Wood, Editor). Florida Game and Freshwater Fish Commission, Tallahassee, USA.

Orians, G. H. and J. F. Whittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:29–49.

SAS Institute. 1985. SAS user's guide: statistics. Version 6 Edition. SAS Institute Inc., Cary, North Carolina, USA.

Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739–747.

Seastedt, T. R. and S. F. Maclean. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. Auk 96:131–142.

Sherrill, D. M. and V. M. Case. 1980. Winter home range of 4 clans of Red-cockaded Woodpeckers in the Carolina Sandhills. Wilson Bulletin 92:369–375.

Skorupa, J. P. and R. W. McFarlane. 1976. Seasonal variation in foraging territory of Red-cockaded Woodpeckers. Wilson Bulletin 88:662–665.

Swihart, R. K. and N. A. Slade. 1985. Influence of sampling interval on estimates of home range size. Journal of Wildlife Management 49:1019–1025.

U.S. Department of Agriculture (USDA). 1995. Final environmental impact statement for the management of the Red-cockaded Woodpecker and its habitat on national forests in the southern region. USDA. Forest Service, Management Bulletin R9-MB 73. Asheville, North Carolina, USA.

U.S. Department of Interior (USDI). 1985. Red-cockaded Woodpecker recovery plan. USDI, Fish and Wildlife Service, Southeast Region, Atlanta, Georgia, USA.

U.S. Department of Interior (USDI). 2003. Red-cockaded Woodpecker recovery plan. USDI, Fish and Wildlife Service, Southeast Region, Atlanta, Georgia, USA.

Walters, J. R., S. J. Daniels, J. H. Carter III, and P. D. Doerr. 2002. Defining quality of Red-cockaded Woodpecker foraging habitat based on habitat use and fitness. Journal of Wildlife Management 66:1064–1082.

Wigley, T. B., S. W. Sweeney, and J. R. Sweeney. 1999. Habitat attributes and reproduction of Red-cockaded Woodpeckers in intensively managed forests. Wildlife Society Bulletin 27:801–809.

Wood, D. A. 1983. Foraging colony habitat characteristics of the Red-cockaded Woodpecker in Oklahoma. Pages 51–58 *in* Red-cockaded Woodpecker Symposium II (D. A. Wood, Editor). Florida Game and Freshwater Fish Commission, Tallahassee, USA.

Wood, D. R. 2001. Multi-resolution assessment of the foraging and reproductive ecology of Red-cockaded Woodpeckers in a Mississippi loblolly-shortleaf pine forest. Dissertation. Mississippi State University, Starkville, USA.

Wood, D. R., F. J. Vilella, and L. W. Burger Jr. 2001. Red-cockaded Woodpecker banding at Bienville National Forest, Mississippi. North American Bird Bander 26:16–19.

Wood, D. R., L. W. Burger Jr., and F. J. Vilella. 2005. Red-cockaded Woodpecker (*Picoides borealis*) behavior in a Mississippi loblolly-shortleaf pine forest. Journal of the Mississippi Academy of Sciences 50:168–176.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Zwicker, S. M. and J. R. Walters. 1999. Selection of pines for foraging by Red-cockaded Woodpeckers. Journal of Wildlife Management 63:843–852.

The Wilson Journal of Ornithology 120(4):801–812, 2008

QUALITY OF ANTHROPOGENIC HABITATS FOR GOLDEN-WINGED WARBLERS IN CENTRAL PENNSYLVANIA

JACOB E. KUBEL[1,2,3] AND RICHARD H. YAHNER[1]

ABSTRACT.—Populations of Golden-winged Warblers (*Vermivora chrysoptera*) are declining dramatically in eastern North America. Success of conservation efforts will rely largely upon identification and management of suitable anthropogenic habitats (e.g., harvested forest and utility rights-of-way [ROWs]). We assessed habitat quality among three habitat types in central Pennsylvania by comparing population density, nesting success, and productivity among 1-ha patch clearcuts (clearcut area), a 60-m-wide utility ROW (wide ROW), and a 20-m-wide utility ROW (narrow ROW) in 2002 and 2003. Golden-winged Warblers did not use any portion of the narrow ROW that occurred outside the clearcut area. Density (territories/ha) did not differ either year (all $P \geq 0.20$) between used sectors of the clearcut area (0.47, 0.50) and the wide ROW (0.71, 0.79). Overall nesting success (successful nests/total nests) was not independent ($P = 0.012$) of habitat type (58% in the clearcut area, 15% in the wide ROW). Overall productivity (young fledged/nesting territory) was greater ($P = 0.026$) in the clearcut area (2.38) than in the wide ROW (0.57). Our study raises important questions about the suitability of utility ROWs for Golden-winged Warblers. *Received 25 August 2006. Accepted 22 March 2008.*

Long-term data from the North American Breeding Bird Survey (BBS) indicate the Golden-winged Warbler (*Vermivora chrysoptera*) has been one of the most rapidly declining neotropical migrants in eastern North America over the past 40 years (Sauer et al. 2007). The species is listed internationally as "Near Threatened" (BirdLife International 2004) and nationally as a "Bird of Conservation Concern" (USDI 2002). Regionally, the BBS reports that Golden-winged Warblers have declined in the northeastern United States (USFWS Region 5) at a rate higher than any other bird since 1966 (Sauer et al. 2007). Declines have been especially alarming during the past 15 years (Buehler et al. 2007).

A major cause of decline is decreased availability of early successional forest (Confer 1992, Buehler et al. 2007). The amount of this habitat in eastern North America has decreased during the past 40–60 years through forest maturation, changes in forest-management practices (i.e., shifts from even-aged to uneven-aged management), decreased rates of farm abandonment (reducing the abundance of old-field habitats), and suppression of natural disturbances (e.g., wildfire, tree-felling and flooding by American beaver [*Castor canadensis*]) (Askins 2001, Lorimer 2001, Trani et al. 2001). Wildfire policy is unlikely to change in the foreseeable future, beaver are removed from areas near human habitation, and major windstorms (e.g., hurricanes and tornadoes) have long recurrence intervals in the northeastern United States (Lorimer and White 2003). Thus, extensive increases in early successional forest are unlikely to occur by "natural" means. Successful conservation of Golden-winged Warblers and other early successional wildlife will rely, in part, on improved quality of existing habitats or increased availability of anthropogenic habitats, such as utility rights-of-way (ROWs) and recently harvested forest stands (Klaus and Buehler 2001, DeGraaf and Yamasaki 2003, Buehler et al. 2007).

No published studies have attempted to assess relative qualities of anthropogenic habitats for breeding populations of Golden-winged Warblers. Therefore, we examined habitat use and reproductive success at a site in central Pennsylvania during 2002 and 2003 to provide preliminary information about the subject. The objective of our study was to evaluate habitat quality among three anthropogenic types by measuring population density, nesting success, and productivity. Our *a priori* assumption was that these measures were indicative of greater habitat quality with the latter two probably of greater importance (Van Horne 1983, Hobbs and Hanley 1990, Brawn and Robinson 1996, Jones et al. 2005).

[1] School of Forest Resources, Pennsylvania State University, University Park, PA 16802, USA.

[2] Current address: Natural Heritage and Endangered Species Program, Division of Fisheries and Wildlife, 1 Rabbit Hill Road, Westborough, MA 01581, USA.

[3] Corresponding author; e-mail: jacob.kubel@state.ma.us

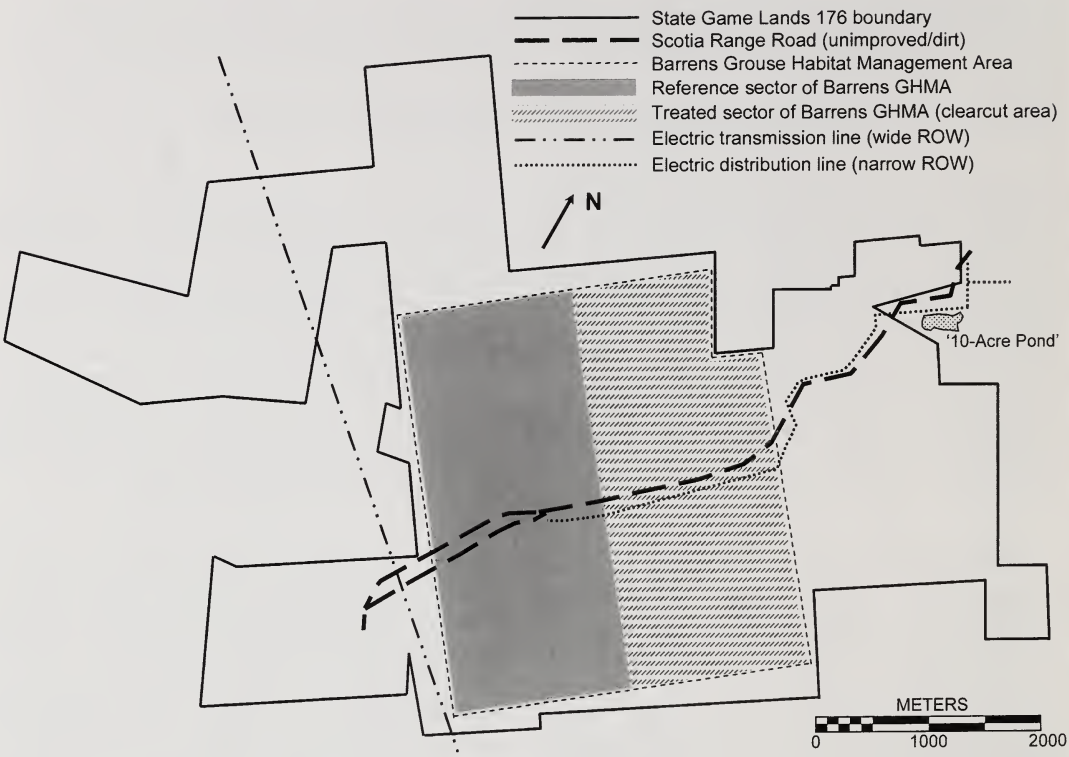


FIG. 1. Habitat types (clearcut area, wide ROW, and narrow ROW) and other features at State Game Lands 176, Centre County, Pennsylvania during 2002 and 2003.

METHODS

Study Area.—Our study was conducted at State Game Lands (SGL) 176 (40° 47′ N, 77° 57′ W) in Centre County, Pennsylvania. This 2,060-ha site has sandy clay soils (Conklin 1943) and consists mainly of aspen (*Populus tremuloides* and *P. grandidentata*) and oak (*Quercus* spp.) cover types (Yahner 1986). Low ridges and a valley characterize the topography, and elevation ranges from a low of ~350 m in the valley to a high of 470 m on the northwest ridge. Numerous forest disturbances have occurred at the site since the 1800s (Conklin 1943) and Golden-winged Warblers have been present since at least 1974 (Yahner 2000, 2003b). The study area is surrounded by agriculture and suburban development.

Habitat Types.—The Pennsylvania Game Commission (PGC) established the Barrens Grouse Habitat Management Area (GHMA) in a 1,126-ha portion of SGL 176 to study the response of Ruffed Grouse (*Bonasa umbellus*) to manipulation of habitat via small-scale, rotation forest-harvesting (Palmer 2003, Yahner 2003b). The Barrens GHMA consists of a 544-ha treated (systematic, 1-ha patch clearcutting) sector and a 582-ha reference (uncut) sector (Palmer 2003; Fig. 1); early successional habitat in 136 recent clearcuts of the treated sector (Fig. 2) represents the first habitat type studied. Each of these 1-ha plots was cut during winters 1999–2001 and retained ~5–25 overstory trees, representing a two-aged regeneration method known as "clearcutting with reserves" (Helms 1998). We refer to the treated sector of the Barrens GHMA as "the clearcut area" to reflect the type of early successional habitat present (i.e., clearcuts and associated access roads and log landings). We defined early successional habitat as having an open canopy; this stage of succession is consistent with that described for habitat requirements of Golden-winged Warblers (i.e., patches of herbs, shrubs, and scattered trees adjacent to a forest [closed-canopy] edge [Confer

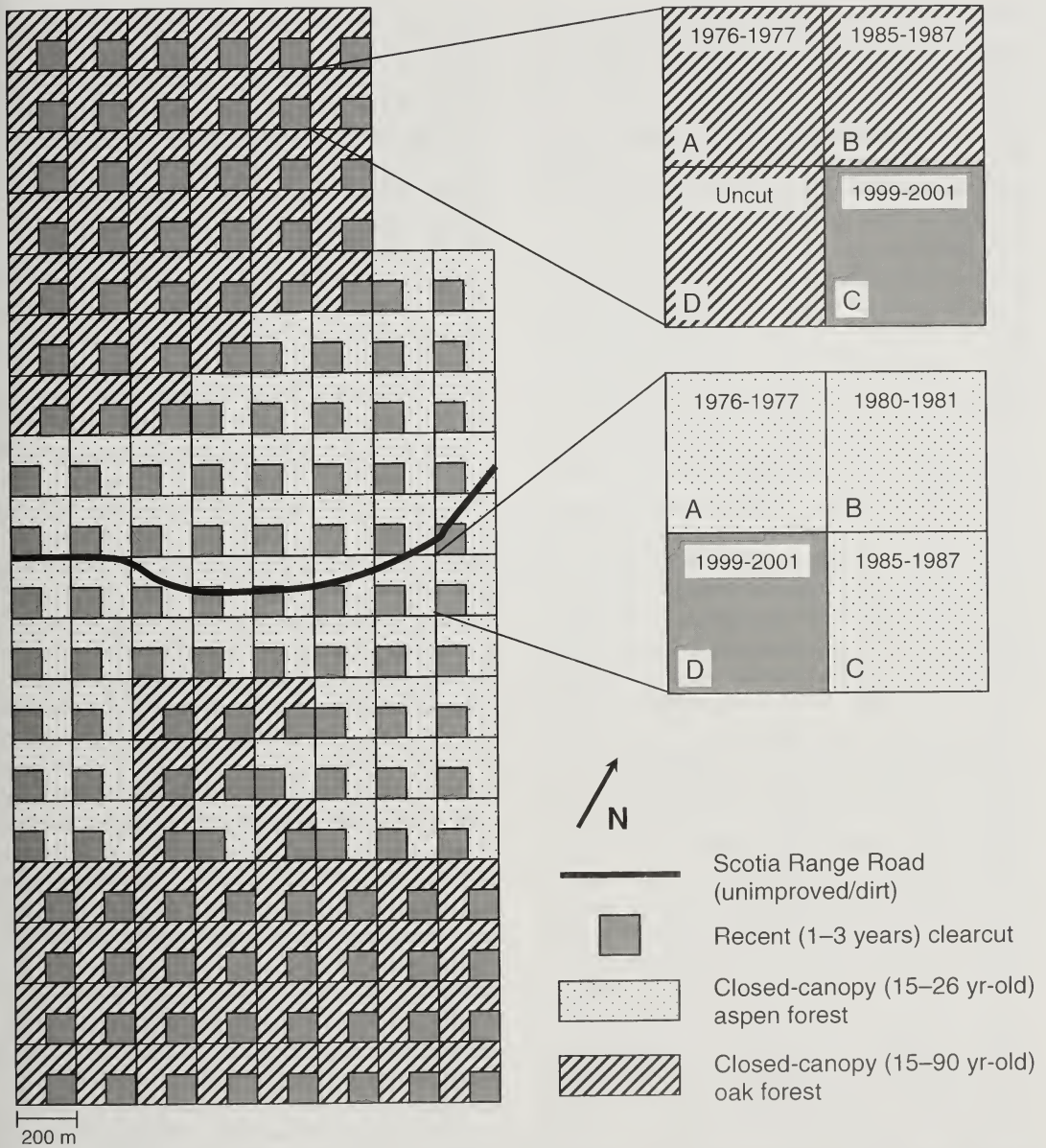


FIG. 2. Schematic and cutting cycles of the clearcut area at the Barrens Grouse Habitat Management Area, Centre County, Pennsylvania, 2002–2003. Management units consisted of 136 blocks subdivided into 1-ha plots (A–D); dates indicate the winter season(s) during which plots were harvested.

1992]). Major vegetation in the regenerating clearcuts included aspen, scrub oak (*Q. ilicifolia*), dwarf chinkapin oak (*Q. prinoides*), tatarian honeysuckle (*Lonicera tatarica*), grasses, and forbs (especially goldenrod [*Solidago* spp.]) in aspen forest, and oak, red maple (*Acer rubrum*), grasses, and ferns (especially hayscented fern [*Dennstaedtia punctilobula*]) in oak forest (Kubel 2005).

The second habitat type was a 3.7-km portion of a 60-m-wide electric transmission line ROW, 2 km west of the clearcut area and termed "the wide ROW" (Fig. 1). Penelec Operating Company of FirstEnergy Corporation maintains the wide ROW by selective herbicide-application at 5-year intervals. Forest types bordering the wide ROW are aspen (southern 60% of the ROW) and oak (northern

40%). Vegetation within the ROW consists primarily of scrub oak, American hazelnut (*Corylus americana*), tatarian honeysuckle, hawthorns (*Craetagus* spp.), grasses, and forbs in aspen forest, and brambles (*Rubus* spp.), blueberry (*Vaccinium* sp.), sweetfern (*Comptonia peregrina*), grasses, and ferns in oak forest (Kubel 2005).

A 20-m-wide electric distribution line ROW bisects the clearcut area and continues in a northerly direction through the northeast corner of SGL 176 (Fig. 1). We considered the portion of the ROW in the clearcut area as part of the clearcut habitat type because the ROW occurred within and immediately adjacent to harvested stands. The portion outside the clearcut area (beginning ~250 m east of the eastern boundary of the clearcut area and continuing 2.4 km northeastward past 10-Acre Pond; Fig. 1) served as the third habitat type and is "the narrow ROW." The narrow ROW has been maintained by selective herbicide-application at 8-year intervals. Vegetation in the narrow ROW is similar to that of aspen forest in the wide ROW and the clearcut area.

Warbler Density.—We used three methods to sample male Golden-winged Warblers during peak territorial and nesting behavior (mid-May through mid-Jun in Pennsylvania; McWilliams and Brauning 2000) in 2002 and 2003. We used each method throughout the three habitat types studied and throughout the sampling season. Particular surveys for each method were conducted independently.

The first sampling method combined point-count surveys (variable circular plot; Reynolds et al. 1980) with playback recordings using a technique modified from Yahner and Ross (1995). A point count comprised (1) a 3.0-min pre-playback period, (2) a 1.3-min playback stimulus period, and (3) a 3.0-min post-playback period (total = 7.3 min), whereupon all male warblers observed by sight and sound during the count were noted. The playback period consisted of seven Type I (Gill and Lanyon 1964, Ficken and Ficken 1967) Golden-winged Warbler songs broadcast at 10-sec intervals with the use of a custom-made compact disc provided by the Macaulay Library of Natural Sounds (Ithaca, NY, USA; MLNS Job #2002073) and a small compact disc player with portable speakers. Each song consisted of one *zee* note and three *bee* notes because this song structure produces a relatively strong response from Golden-winged Warblers (Ficken and Ficken 1973). Songs were broadcast at a volume comparable to that of male warblers on the study area.

We conducted point counts in the clearcut area at stations (n = 64 in 2002 and 44 in 2003) distributed among four transects with each transect spaced 400 m apart. Stations in the wide ROW (n = 15 in 2002 and 18 in 2003) and the narrow ROW (n = 12 in 2002 and 0 in 2003) were distributed along a single transect positioned along the central axis of each ROW. Point-count stations were spaced 200 m apart along a given transect. Lengths of transects in 2002 and 2003, respectively, were 3.2 and 2.0 km in the clearcut area, 2.9 and 3.5 km in the wide ROW, and 2.2 and 0.0 km in the narrow ROW. We defined a point-count survey as the sampling of all stations at SGL 176 once within 7 days; JEK conducted four and three surveys in 2002 and 2003, respectively. Surveys were conducted during 20 May–17 June between dawn and 1000 hrs EST when wind velocity was <16 km/hr and precipitation was absent or limited to light, intermittent rain.

The second and third sampling methods were spot-mapping methods and supplemented the point-count surveys. The first spot-mapping method, termed the "opportunistic" method, was similar to the "Combined Version" mapping method (Paul and Roth 1983) and was used daily from 4 May to 26 June in 2002 and 2003. This method consisted of five or more visits (0.2–3.0 hrs each) over the course of the breeding season to specific areas where Golden-winged Warblers were known to occur. We recorded movements and behaviors of individual warblers, giving particular attention to interactions among males that might help identify boundaries of territories (Robbins 1970).

The second spot-mapping method, termed the "census" method, was modified from that recommended by the International Bird Census Committee (Robbins 1970) and was used eight and seven times (~twice/week, 22 May–18 Jun) in the clearcut area and the wide ROW, respectively, in 2003. Each census entailed walking slowly (<3.2 km/hr) along predetermined routes and recording location, time, gender, and behavior of all Golden-

winged Warblers seen or heard in an attempt to obtain a complete count of males within the point-count survey area. Censuses occurred between dawn and 1000 hrs EST during days with little or no precipitation and winds <16 km/hr. Observer, starting point, and direction of travel for each route alternated throughout the season, and we took special precautions to avoid double-counting individual birds located between routes (Kubel 2005).

We were usually able to differentiate individuals of neighboring territories during a given sampling method by observing singing males simultaneously. We also gave particular attention to plumage (e.g., hybrid vs. "pure") and song (e.g., pitch, length, and number of notes) of each individual observed. For example, several individuals having distinctly "raspy" songs relative to most warblers on the study area were encountered consistently in particular clearcuts and portions of the wide ROW. Several other individuals having unusually "fast" songs (i.e., especially short notes without compensatory increases in length of interval between notes) were encountered consistently in particular areas. One territory consisted of a male that consistently sang an unusually high number (6–7) of *bee* notes, and the *bee* notes of males at several other territories seemed to be higher-pitched than the introductory *zee* note (*bee* notes were lower-pitched than *zee* notes in all other males).

We combined results from point-count and spot-mapping surveys to estimate total number of territories in each habitat type. In designating a territory, the International Bird Census Committee (Robbins 1970) recommended that of 8–10 visits to a survey area, at least three observations of an individual in a particular region of the area should be registered to count the region as a territory. We made more than 10 visits (combining point counts and spot-mapping) to survey areas of each habitat type and arbitrarily required at least five observations of a male Golden-winged Warbler in a particular region for it to be designated a territory. We also required the five observations to occur during a period of ≥2 weeks (to account for possible migrants) because visits often occurred at short intervals (1–5 days).

We did not detect Golden-winged Warblers throughout all sectors of each habitat type. We were unable to ascertain whether apparent absence from certain sectors was due to those sectors being unsuitable (not available) versus not preferred (available but not selected; Johnson 1980). We were unable to identify what constituted available habitat and based estimates of density on the used sector of each habitat type. We defined "used sector" as the area inclusive of all known warbler territories and exclusive of areas where warblers were not observed. We calculated density for each habitat type as number of territories/ha of early successional habitat present in the used sector.

Nesting Success and Productivity.—We conducted nest searching in the clearcut area and the wide ROW during 2002 and 2003 by observing warbler behaviors indicative of mated status or locations of nests (Baird 1967; Ficken and Ficken 1967, 1968a, 1968b; Confer 1992) and by physically searching potential nest substrates (e.g., patches of herbaceous vegetation) with a three-pronged stick (J. L. Confer, pers. comm.). We coordinated nest searching with opportunistic spot-mapping and usually spent 0.5–2.0 hrs/visit searching a territory for nests.

Locations of nests discovered by observers other than JEK were marked temporarily (≤24 hrs) by attaching plastic flagging to a shrub ≥10 m from the nest; no other nests were marked. JEK monitored each nest through completion (i.e., fledging or failure) by visiting the nest at 3-day intervals (Martin and Geupel 1993) and observing its contents; special care was taken to avoid leaving visual and olfactory clues to nest location. Nests were checked daily when nestlings were near fledging (within 1–3 days, based on expected fledging date of 8–11 days post-hatch [Will 1986, Confer et al. 2003]) to maximize chances of confirming successful fledging by observation of fledged individuals.

We estimated nesting success for each habitat type using apparent success (Shaffer 2004) and nest survival rate (Mayfield 1961, 1975). We calculated apparent success by dividing number of successful nests (nests that fledged ≥1 young) by total number of nests for which nest fate was known. We included nests where we failed to observe eggs or nestlings in unsuccessful nests (those not fledging young) in the total if we had observed them during the building stage and nest construction had been completed (Klaus and Buehler

TABLE 1. Amount (ha) of early successional habitat, number of observed territories, and density of Golden-winged Warblers in used sectors of the clearcut area and the wide ROW at State Game Lands 176, Centre County, Pennsylvania, 2002 and 2003. Goodness-of-fit tests were used to compare observed vs. expected number of territories between used sectors of the clearcut area and the wide ROW each year.

	Amount of habitat		Observed territories (*n*)		Density[a]			
Year	Clearcut	ROW	Clearcut	ROW	Clearcut	ROW	χ^2	*P*
2002	61.9	12.6	29	9	0.47	0.71	1.25	0.264
2003			31	10	0.50	0.79	1.64	0.200

[a] Density = territories/ha of early successional habitat.

2001) or there was physical evidence the nest had been depredated (e.g., nest was overturned or destroyed). We calculated nest survival rate by multiplying survival rates of egg-laying, incubation, and nestling stages of the nesting cycle (Mayfield 1961, 1975). We assigned 3, 11, and 8 exposure days to the egg-laying, incubation, and nestling stages, respectively (Will 1986, Confer 1992, Confer et al. 2003, Kubel 2005), based on a half-day for the first and last days of each stage and a full day for each day in between. We used data only from nests in which eggs and/or nestlings were observed in calculating survival rates.

We estimated productivity for each habitat type by calculating mean number of fledglings produced per nesting territory, which we defined as a territory within which at least one nesting attempt occurred. We assumed when a nest was successful that number of young fledged was equal to the number of nestlings last observed in the nest (Confer et al. 2003).

Statistical Analyses.—Statistical comparisons of density, nesting success, and productivity among habitat types were restricted to the clearcut area and the wide ROW because we did not detect Golden-winged Warblers in the narrow ROW. Statistical tests were considered significant at $P \leq 0.05$.

We compared density between used sectors of the clearcut area and the wide ROW by comparing observed versus expected numbers of territories with Chi-square goodness-of-fit tests (Sokal and Rohlf 1995). We calculated 95% confidence intervals (CI) for apparent success, nest survival rate, and productivity in the clearcut area and the wide ROW. We used Pearson Chi-square tests-of-independence (Minitab Inc. 1998), program CONTRAST (Hines and Sauer 1989), and Mann-Whitney *U*-tests (Sokal and Rohlf 1995, Systat Software Inc. 2002) to compare apparent success, nest survival rate, and productivity, respectively, between the clearcut area and the wide ROW.

RESULTS

Density.—We did not detect Golden-winged Warblers in the narrow ROW and we assumed density in the habitat type was 0.00 territories/ha. We estimated that 29 and 31 territories occurred in the clearcut area, and 9 and 10 territories occurred in the wide ROW in 2002 and 2003, respectively; almost all territories occurred in aspen forest. Density was 0.47 and 0.50 territories/ha in the clearcut area and 0.71 and 0.79 in the wide ROW in 2002 and 2003, respectively, based on early successional cover in used sectors of each habitat type (Table 1). Observed versus expected number of territories did not differ between used sectors of the clearcut area and the wide ROW in either year ($\chi^2 \leq 1.64$, df = 1, $P \geq 0.20$; Table 1).

Nesting Success.—We analyzed data for 9 and 15 nests monitored in the clearcut area and 6 and 7 nests in the wide ROW in 2002 and 2003, respectively. Apparent success was 33% in 2002 and 73% in 2003 in the clearcut area, and 17% in 2002 and 14% in 2003 in the wide ROW (Fig. 3). Success during both years combined was not independent (χ^2 = 6.34, df = 1, $P = 0.012$) of habitat type (58% [95% CI = 37–78%] in the clearcut area and 15% [95% CI = 2–45%] in the wide ROW).

We excluded five nests from calculations of nest survival rate because no exposure days were observed (4 nests [wide ROW, 2002] observed during the building stage appeared to have been depredated before eggs were observed, and the other [clearcut area, 2003] appeared to have been abandoned [with eggs] prior to discovery). Survival rates in 2002 and 2003, respectively, were 4% (n = 9 nests) and

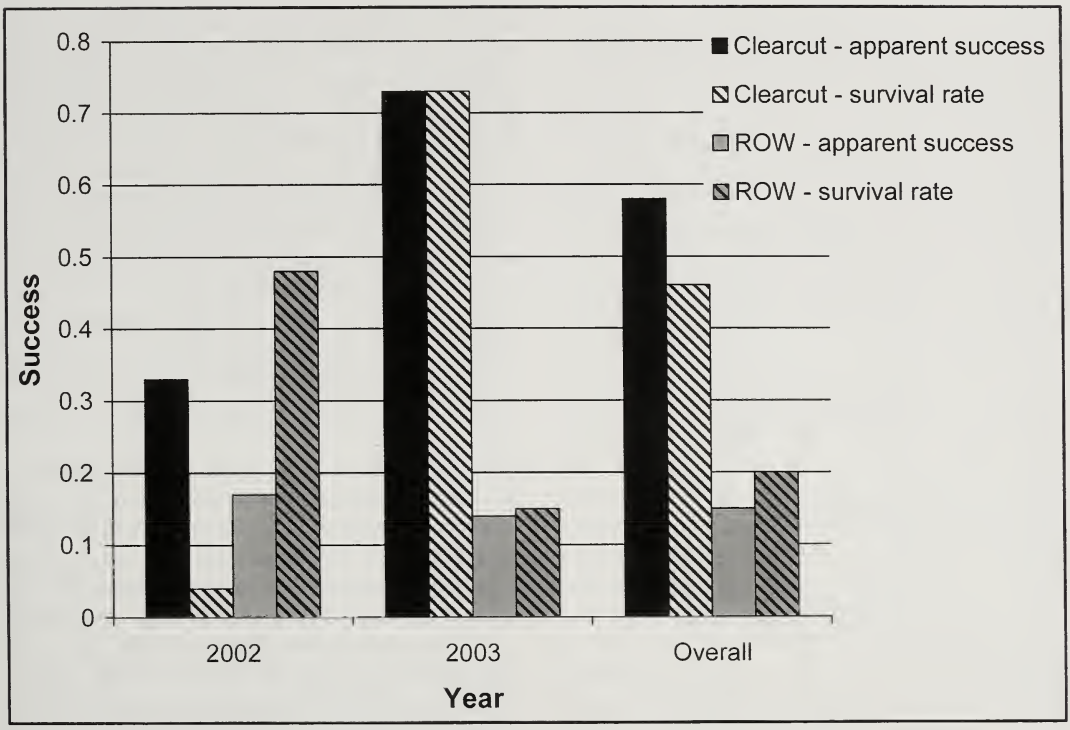


FIG. 3. Estimates of nesting success in the clearcut area and the wide ROW at State Game Lands 176, Centre County, Pennsylvania during 2002 and 2003. Estimates included apparent success (proportion of nests fledging young) and nest survival rate (Mayfield 1961, 1975). Apparent success was a more reliable estimate in 2002 because nest survival rate was overestimated in the wide ROW (4 depredated nests excluded from analysis) and underestimated in the clearcut area (3 nests survived to fledging, and 4% survival would imply 75 nesting attempts among only 8 breeding pairs). Apparent success overall differed ($P = 0.012$) between habitat types.

73% ($n = 14$) in the clearcut area, and 48% ($n = 2$) and 15% ($n = 7$) in the wide ROW (Table 2; Fig. 3). Survival rates differed ($\chi^2 = 8.75$, df = 1, $P = 0.003$) between habitat types in 2003 but did not differ ($\chi^2 = 2.08$, df = 1, $P = 0.15$) over both years combined (46% [95% CI = 28–76%] in the clearcut area and 20% [95% CI = 6–67%] in the wide ROW) (Table 2). Survival rate did not differ between years in the wide ROW ($\chi^2 = 0.74$, df = 1, $P = 0.39$) but was greater in 2003 than in 2002 in the clearcut area ($\chi^2 = 18.5$, df = 1, $P < 0.001$).

Nest predation was the primary cause of nest failure in both habitat types in 2002, accounting for five of six (83%) failures in the clearcut area and all five (100%) failures in the wide ROW. Nest predation in 2003 caused only one of four (25%) failures in the clearcut area compared to six of six (100%) failures in the wide ROW.

Productivity.—We estimated there were 28 nesting territories in the clearcut area and the wide ROW combined over both years of the study. Productivity in 2002 and 2003, respectively, was 1.13 ($n = 8$ nesting territories) and 3.15 ($n = 13$) fledglings/nesting territory in the clearcut area and 0.67 ($n = 3$) and 0.50 ($n = 4$) in the wide ROW. Productivity during both years combined was different ($U = 114$, $P = 0.026$) between habitat types (2.38 [95% CI = 1.53–3.24] in the clearcut area and 0.57 [95% CI = 0.00–1.47] in the wide ROW). Productivity was similar between years in the wide ROW ($U = 6.5$, $P = 0.83$) but greater in 2003 than in 2002 in the clearcut area ($U = 82.5$, $P = 0.018$).

DISCUSSION

Lack of replication and short duration of the study limit the interpretation and application of our results. However, our intensive survey ef-

TABLE 2. Estimates of nest survival rate (daily, stage, and overall; Mayfield 1961, 1975) for breeding Golden-winged Warblers in the clearcut area and the wide ROW at State Game Lands 176, Centre County, Pennsylvania, 2002 and 2003. The overall rate was compared between habitat types (by year) using program CONTRAST (Hines and Sauer 1989).

			Daily survival[a]			Stage survival[b]						
Year	Habitat	Nests (n)	E	I	N	E	I	N	Overall survival[c]	Overall SE	Overall 95% CI	χ^2	P
2002	Clearcut	9	0.60	0.90	0.94	0.22	0.33	0.62	0.04	0.09	0.00–0.55	1.44	0.230
	ROW	2	1.00	0.94	1.00	1.00	0.48	1.00	0.48	0.35	0.13–1.00		
2003	Clearcut	14	0.94	0.99	1.00	0.82	0.90	1.00	0.73	0.13	0.52–1.00	8.75	0.003
	ROW	7	0.82	0.95	0.92	0.55	0.54	0.51	0.15	0.15	0.03–0.74		
Combined	Clearcut	23	0.91	0.97	0.98	0.75	0.71	0.86	0.46	0.12	0.28–0.76	2.08	0.149
	ROW	9	0.83	0.94	0.95	0.57	0.52	0.67	0.20	0.14	0.06–0.67		

[a] Daily survival = 1 – (nest failures/observation days). Values are probabilities of nest survival over 24 hrs by egg-laying (E), incubation (I), and nestling (N) stages.
[b] Stage survival = (daily survival)$^{\text{stage length}}$, where stage length is 3, 11, and 8 days for E, I, and N, respectively. Values are probabilities of nest survival through egg-laying (E), incubation (I), and nestling (N) stages.
[c] Overall survival = E × I × N (of stage survival) given as probabilities of nest survival over all stages.

forts likely produced accurate estimates of habitat use and reproductive success at SGL 176 during the study, as we thoroughly monitored the entire breeding population within each habitat type and found a high percentage of nests (likely ≥85% during 2003, based on ability to identify mated status of males by singing behavior; Ficken and Ficken 1967). Close inspection of our results yields interesting hypotheses that have range-wide implications and warrant further investigation, especially considering the importance of appropriate habitat management for Golden-winged Warblers and other early-successional, ground-nesting birds in eastern North America.

Clearcut Area and Wide ROW.—Densities of singing males observed within the used sectors of the clearcut area and the wide ROW in 2002 and 2003 suggest the two habitat types are suitable when appropriate nesting substrates and other resources are present (e.g., in aspen forest; Kubel 2005). However, reproductive success was vastly different between types during our study because rates of nest predation were much lower in the clearcut area than in the wide ROW. This result is surprising because the two habitat types were <2 km apart and in the same patch of forest (SGL 176 is surrounded by agriculture and development); we would not expect predator communities to differ between those sectors of the study area.

We can only speculate about the identity of nest predators and why nest predation differed between the clearcut area and the wide ROW, but there is fairly strong evidence to suggest that nest predators differed between habitat types. Almost all depredated nests in the clearcut area were undamaged by the predator. Observations of snakes and of avian predators at ground level were rare, but eastern chipmunks (*Tamias striatus*) were observed frequently near (1–10 m) nests. Chipmunks were unusually abundant in 2002 both at SGL 176 (Yahner 2003a; JEK, pers. obs.) and regionally (J. L. Confer, pers. comm.), but appeared to be much less abundant in 2003. Major inter-annual population fluctuations are common in small mammals, which might explain why nest predation in the clearcut area was considerably lower in 2003 (7%) relative to 2002 (56%).

Nest predation in the wide ROW was high

in both 2002 (83%) and 2003 (86%) and did not follow the pattern observed in the clearcut area. Physical evidence at almost half of the depredated nests in the wide ROW suggested predators other than small mammals and snakes, as five nests were severely damaged (e.g., pulled apart, flipped over, and/or pressed into the ground) and vegetation surrounding an additional nest was trampled. Larger avian predators (e.g., American Crow [*Corvus brachyrhynchos*] and Blue Jay [*Cyanocitta cristata*]) were rarely seen at the wide ROW. Therefore, mid- to large-sized mammals likely had an important role in nest predation at this habitat type.

Nest predation may have been high in the wide ROW because long-term management of this habitat by selective herbicide treatment has resulted in a static vegetation structure with abrupt edges between patches of shrubs and herbs. This simple structure is easier to traverse than one with gradual edges where plant succession occurs at high levels of spatial heterogeneity and poses a physical barrier to movement (Bowman and Harris 1980, Yahner and Wright 1985, Suarez et al. 1997). We observed animal trails in the wide ROW, and the trails tended to avoid patches of shrubs and travel through open patches of herbs. Hence, mid- to large-sized mammals at the wide ROW were often within close proximity of nests of Golden-winged Warblers, as nests were usually in patches of herbaceous vegetation (Kubel 2005). Animal trails were not encountered in harvested stands of the clearcut area where these relatively new, ephemeral shrublands tended to have greater interspersion of shrubs and herbs. This complex vegetation structure is unlikely to impede movement of small mammals, which we suspect were the primary nest predators in the clearcut area.

Proximity to agriculture may be an additional explanation for differences in nest predation between the clearcut area and the wide ROW during our study. Predation pressure may be greater in agricultural landscapes than in forested landscapes (Andrén and Angelstam 1988, Andrén 1992, Rudnicky and Hunter 1993), or greater at agricultural edges than at silvicultural edges (Bayne and Hobson 1997, Rodewald and Yahner 2001). Abundance of meso-carnivores in particular can be relatively high in agricultural areas (Pedlar et al. 1997, Dijak and Thompson 2000). Stands used by Golden-winged Warblers in the clearcut area were 1.0–2.6 km from agriculture, whereas used portions of the wide ROW were only 0.0–0.6 km distant.

The high rate of nest success in the clearcut area in 2003 is similar to the ≥83% success observed for ground nests (≤0.5 m) of multiple avian species in young (≤10 yrs), even-aged aspen stands at the same site during 1985–1987 (Yahner 1991). King et al. (2001) observed a daily survival rate of 0.990 for 290 nests of multiple species in clearcuts in New Hampshire, which is comparable to the daily survival rate of nests of Golden-winged Warblers in the clearcut area in 2003. Thus, clearcutting at SGL 176 and elsewhere in the northeastern United States may create high-quality habitat for Golden-winged Warblers and other ground-nesting birds.

Some studies of avian ecology in utility ROWs have reported higher nest success for shrubland birds than we observed for Golden-winged Warblers in the wide ROW at SGL 176. Reported estimates of nest success in ROWs throughout the northeastern United States include 83% for Chestnut-sided Warblers (*Dendroica pensylvanica*) in Massachusetts (King and Byers 2002), 56 and 61% for 20 species in Maryland (Chasko and Gates 1982), 55% for multiple species in Maine, Massachusetts, and New York (Confer and Pascoe 2003), and 39 and 65% for 10 species in Pennsylvania (Yahner et al. 2004). These estimates of nest success include data from numerous shrub-nesting species and do not necessarily reflect success of ground-nesting species like the Golden-winged Warbler.

We are not aware of any published studies of nest success specific to Golden-winged Warblers in ROW habitat, but estimates from research through 2005 included 36% in West Virginia (R. A. Canterbury, unpubl. data), 41% in New York (J. L. Confer, unpubl. data), and 44% in New Jersey (Sharon DeFalco, unpubl. data) with almost all failures the result of nest predation. As in our study, these estimates are lower than those reported for Golden-winged Warblers in other habitats, which include 55% in mowed field-forest edges and rocky outcrops of the Canadian Shield (Rachel Vallender and R. J. Robertson, unpubl. data), 71% in upland mine fields and edges

(R. A. Canterbury, unpubl. data), 73% along access roads and logging decks in young (<20 yrs) forest stands (Klaus and Buehler 2001), and 85% in brushy fields adjacent to forest (Will 1986). An additional estimate from upland mine fields (Bulluck and Buehler 2008) ranges from 50% (overall nest survival based on daily survival rate of 0.973) to 59% (apparent nest success). Confer et al. (2003) reported only 38% nest success in shrubby fields of abandoned croplands but, perhaps success there was influenced by the agricultural history and setting of the study sites.

Narrow ROW.—Structure and species composition of vegetation in the narrow ROW were similar to that observed in aspen sectors of the wide ROW and the clearcut area (Kubel 2005). However, our surveys in 2002 failed to detect Golden-winged Warblers in the portion of the narrow ROW that served as our third habitat type. Preliminary surveys in 1998 and 1999 (RHY, unpubl. data) failed to detect Golden-winged Warblers in the narrow ROW, and we concluded prior to 2003 the species does not typically establish territories there. Warblers did establish territories and nests in portions of the same ROW where it extended into the clearcut area (surveyed incidentally as part of the clearcut area in 2002 and 2003), suggesting that additional openings contiguous with the ROW were required for breeding. We are not aware of any published studies that have documented territories of Golden-winged Warblers in narrow (≤20-m) ROWs bordered on both sides by relatively mature (≥40 yrs) forest. However, this warbler does occur along a portion of a 20-m-wide ROW in southern New York (J. L. Confer, pers. comm.) where there are additional openings in the forest canopy adjacent to both sides of the ROW (Kubel 2005).

Rossell (2001) suggested Golden-winged Warblers choose song perches at positions in the forest canopy that enhance their ability to display vocally and visually to attract mates. Most territories in the wide ROW at SGL 176 were 100–175 m long; thus, a territory in the narrow ROW would have to be 300–525 m long to contain as much early successional cover. Assuming there is a minimum threshold for amount of early successional habitat in a territory, a non-linear habitat would optimize the ability of a male to be conspicuous in all parts of the territory by visual and vocal displays (e.g., for mate attraction or territory defense). This may explain why Golden-winged Warblers at SGL 176 and elsewhere (e.g., southern New York) use portions of 20-m-wide ROWs only where they are contiguous with or adjacent to other forest openings.

CONSERVATION IMPLICATIONS

Small-scale, rotation clearcutting may be a favorable management technique for Golden-winged Warblers when suitable regeneration (i.e., small, interspersed patches of herbs and multi-stemmed shrubs or root-suckering trees [Kubel 2005]) can be assured. However, caution should be used when assessing the potential for ROWs to provide suitable habitat. Narrow ROWs (≤20-m wide) in the setting of mature (80–90 yrs) forest and in the absence of additional open areas should not be regarded as potential sources of habitat during conservation planning. Wider (e.g., 60-m wide) ROWs appear to provide habitat, but our study raises questions about whether nests of Golden-winged Warblers (and perhaps other ground-nesting birds) may be especially vulnerable to nest predation by mid- to large-sized mammals in certain types of ROWs. Further, ROWs do not appear to be preferred habitats in some areas (Bulluck and Buehler 2006).

Our results are not necessarily representative of long-term conditions at SGL 176, but the low reproductive success we observed in the wide ROW appears to be consistent with relatively low success observed for Golden-winged Warblers in ROWs elsewhere in the eastern United States. Further research is needed to learn if ROWs may act as habitat sinks for Golden-winged Warblers, especially where ROWs are maintained in a manner that creates abrupt edges between patches of shrubs and herbs. We recommend long-term monitoring of reproductive success coupled with experimental manipulations of vegetation structure.

ACKNOWLEDGMENTS

Funding was provided by the Teresa Heinz Scholars for Environmental Research and the Pennsylvania Agricultural Experiment Station. We thank J. A. DeCecco, M. E. McDermott, D. C. Rabbers, K. E. Vilberg, and P. L. Howell for field assistance, M. R. Mar-

shall and C. B. Goguen for help in study design and data analysis, J. L. Confer for advice on nest-searching techniques, and M. C. Brittingham, K. C. Steiner, and two anonymous reviewers for helpful comments on earlier versions of this manuscript. We appreciate assistance from Loren Zirkle of Allegheny Power, and Matt Belinda and Charles Olenik of FirstEnergy.

LITERATURE CITED

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

Andrén, H. and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69:544–547.

Askins, R. A. 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildlife Society Bulletin 29:407–412.

Baird, J. 1967. Some courtship displays of the Golden-winged Warbler. Wilson Bulletin 79:301–306.

Bayne, E. M. and K. A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. Conservation Biology 11:1418–1429.

BirdLife International. 2004. *Vermivora chrysoptera*. *In* 2007 IUCN Red List of Threatened Species. www.iucnredlist.org (accessed 24 February 2008).

Bowman, G. B. and L. D. Harris. 1980. Effect of spatial heterogeneity on ground-nest depredation. Journal of Wildlife Management 44:806–813.

Brawn, J. D. and S. K. Robinson. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. Ecology 77:3–12.

Buehler, D. A., A. M. Roth, R. Vallender, T. C. Will, J. L. Confer, R. A. Canterbury, S. Barker Swarthout, K. V. Rosenberg, and L. P. Bulluck. 2007. Status and conservation priorities of Golden-winged Warbler (*Vermivora chrysoptera*) in North America. Auk 124:1439–1445.

Bulluck, L. P. and D. A. Buehler. 2006. Avian use of early successional habitats: are regenerating forests, utility right-of-ways and reclaimed surface mines the same? Forest Ecology and Management 236:76–84.

Bulluck, L. P. and D. A. Buehler. 2008. Factors influencing Golden-winged Warbler (*Vermivora chrysoptera*) nest-site selection and nest survival in the Cumberland Mountains of Tennessee. Auk 125: In Press.

Chasko, G. G. and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. Wildlife Monographs 82.

Confer, J. L. 1992. Golden-winged Warbler (*Vermivora chrysoptera*). The birds of North America. Number 20.

Confer, J. L. and S. M. Pascoe. 2003. Avian communities on utility rights-of-ways and other managed shrublands in the northeastern United States. Forest Ecology and Management 185:193–205.

Confer, J. L., J. L. Larkin, and P. E. Allen. 2003. Effects of vegetation, interspecific competition, and brood parasitism on Golden-winged Warbler (*Vermivora chrysoptera*) nesting success. Auk 120:138–144.

Conklin, W. G. 1943. Portion of famous "Barrens" in Centre County acquired as state game lands. Pennsylvania Game News 14:6–7, 24–25.

DeGraaf, R. M. and M. Yamasaki. 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. Forest Ecology and Management 185:179–191.

Dijak, W. D. and F. R. Thompson III. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. Journal of Wildlife Management 64:209–216.

Ficken, M. S. and R. W. Ficken. 1967. Singing behaviour of Blue-winged and Golden-winged warblers and their hybrids. Behaviour 28:149–181.

Ficken, M. S. and R. W. Ficken. 1968a. Courtship of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. Wilson Bulletin 80:161–172.

Ficken, M. S. and R. W. Ficken. 1968b. Territorial relationships of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. Wilson Bulletin 80:442–451.

Ficken, M. S. and R. W. Ficken. 1973. Effect of number, kind and order of song elements on playback responses of the Golden-winged Warbler. Behaviour 46:114–128.

Gill, F. B. and W. E. Lanyon. 1964. Experiments on species discrimination in Blue-winged Warblers. Auk 81:53–64.

Helms, J. A. 1998. The dictionary of forestry. Society of American Foresters, Washington, D.C., USA.

Hines, J. E. and J. R. Sauer. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery rate estimates. Fish and Wildlife Technical Report 24. USDI, Fish and Wildlife Service, Washington, D.C., USA.

Hobbs, N. T. and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? Journal of Wildlife Management 54:515–522.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, J., P. J. Doran, L. R. Nagy, and R. T. Holmes. 2005. Relationship between Mayfield nest-survival estimates and seasonal fecundity: a cautionary note. Auk 122:306–312.

King, D. I. and B. E. Byers. 2002. An evaluation of powerline rights-of-way as habitat for early-successional shrubland birds. Wildlife Society Bulletin 30:868–874.

King, D. I., R. M. DeGraaf, and C. R. Griffin. 2001. Productivity of early successional shrubland birds in clearcuts and groupcuts in an eastern deciduous forest. Journal of Wildlife Management 65:345–350.

Klaus, N. A. and D. A. Buehler. 2001. Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Ap-

palachian Mountains. Wilson Bulletin 113:297–301.

KUBEL, J. E. 2005. Breeding ecology of Golden-winged Warblers in managed habitats of central Pennsylvania. Thesis. Pennsylvania State University, University Park, USA.

LORIMER, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildlife Society Bulletin 29:425–439.

LORIMER, C. G. AND A. S. WHITE. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management 185:41–64.

MARTIN, T. E. AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64: 507–519.

MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MCWILLIAMS, G. M. AND D. W. BRAUNING. 2000. The birds of Pennsylvania. Cornell University Press, Ithaca, NY, USA.

MINITAB Inc. 1998. MINITAB for Windows. Version 12.2. Minitab Inc., State College, Pennsylvania, USA.

PALMER, W. L. 2003. The Barrens Grouse Habitat Management Study. State Game Lands Number 176. Pennsylvania Game Commission Project Annual Job Report, Job Code 29001. www.pgc.state.pa.us/pgc/lib/pgc/reports/2003_wildlife/29001-02z.pdf (accessed 6 August 2006).

PAUL, J. T. AND R. R. ROTH. 1983. Accuracy of a version of the spot-mapping census method. Journal of Field Ornithology 54:42–49.

PEDLAR, J. H., L. FAHRIG, AND H. G. MERRIAM. 1997. Raccoon habitat use at 2 spatial scales. Journal of Wildlife Management 61:102–112.

REYNOLDS, R. T., J. M. SCOTT, AND R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

ROBBINS, C. S. 1970. An international standard for a mapping method in bird census work. International Bird Census Committee. Audubon Field Notes 24:722–726.

RODEWALD, A. D. AND R. H. YAHNER. 2001. Influence of landscape composition on avian community structure and associated mechanisms. Ecology 82: 3493–3504.

ROSSELL JR., C. R. 2001. Song perch characteristics of Golden-winged Warblers in a mountain wetland. Wilson Bulletin 113:246–248.

RUDNICKY, T. C. AND M. L. HUNTER. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. Journal of Wildlife Management 57:358–364.

SAUER, J. R., J. E. HINES, AND J. FALLON. 2007. The North American Breeding Bird Survey, results and analysis 1966–2006. Version 10.13.2007. USDI, Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.usgs.gov/bbs/bbs.html (accessed 24 February 2008).

SHAFFER, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

SOKAL, R. R. AND F. J. ROHLF. 1995. Biometry. Third Edition. W. H. Freeman, New York, USA.

SUAREZ, A. V., K. S. PFENNIG, AND S. K. ROBINSON. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conservation Biology 11:928–935.

SYSTAT Software Inc. 2002. SYSTAT grad pack for Windows. Version 10.0. Systat Software Inc., Richmond, California, USA.

TRANI, M. K., R. T. BROOKS, T. L. SCHMIDT, V. A. RUDIS, AND C. M. GABBARD. 2001. Patterns and trends of early successional forests in the eastern United States. Wildlife Society Bulletin 29:413–424.

U. S. DEPARTMENT OF INTERIOR (USDI). 2002. Birds of conservation concern 2002. USDI, Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia, USA.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

WILL, T. C. 1986. The behavioral ecology of species replacement: Blue-winged and Golden-winged warblers in Michigan. Dissertation. University of Michigan, Ann Arbor, USA.

YAHNER, R. H. 1986. Structure, seasonal dynamics, and habitat relationships of avian communities in small even-aged forest stands. Wilson Bulletin 98: 61–82.

YAHNER, R. H. 1991. Avian nesting ecology in small even-aged aspen stands. Journal of Wildlife Management 55:155–159.

YAHNER, R. H. 2000. Long-term effects of even-aged management on bird communities in central Pennsylvania. Wildlife Society Bulletin 28:1102–1110.

YAHNER, R. H. 2003a. Population trends in eastern chipmunks: implications to avian nesting success. Journal of the Pennsylvania Academy of Science 76:62–65.

YAHNER, R. H. 2003b. Responses of bird communities to early successional habitat in a managed landscape. Wilson Bulletin 115:292–298.

YAHNER, R. H. AND B. D. ROSS. 1995. Seasonal response of Wood Thrushes to taped-playback songs. Wilson Bulletin 107:738–741.

YAHNER, R. H. AND A. L. WRIGHT. 1985. Depredation on artificial ground nests: effects of edge and plot age. Journal of Wildlife Management 49:508–513.

YAHNER, R. H., B. D. ROSS, R. T. YAHNER, R. J. HUTNIK, AND S. A. LISCINSKY. 2004. Long-term effects of rights-of-way maintenance via the wire-border zone method on bird nesting ecology. Journal of Arboriculture 30:288–294.

The Wilson Journal of Ornithology 120(4):813–819, 2008

AVIAN CELL-MEDIATED IMMUNE RESPONSE TO DROUGHT

J. M. FAIR[1,2] AND S. J. WHITAKER[1]

ABSTRACT.—Regional droughts have far-reaching, substantial, and easily recognizable impacts on populations and the environment. One component of these impacts that is not widely recognized is impairment of immune function by drought-related physiological stress. We studied cell-mediated immune function of cavity-nestling Western Bluebirds (*Sialia mexicana*), Ash-throated Flycatchers (*Myiarchus cinerascens*), and Violet–green Swallows (*Tachycineta thalassina*) at Los Alamos, New Mexico. There was a dramatic decrease in the cell-mediated immune responsiveness of developing nestlings associated with unusually dry conditions. Adult Western Bluebirds captured in 2002 weighed 7% less than in all previous years and average clutch size for all three species was reduced by 21% in 2002. Nestling body mass was also reduced for flycatcher and bluebird nestlings in 2002 compared to all other years. Survival to fledging age was lower overall during the drought years of 2000–2002 compared to the first 3 years of the study. *Received 17 April 2006. Accepted 14 February 2008.*

Regional droughts have far-reaching, substantial, and easily recognizable impacts on populations (George et al. 1992) and the environment (Allen and Breshears 1998). One component of these impacts that is not widely recognized is impairment of immune function by drought-related physiological stress. There is ample evidence that stress affects immune system function (Apanius 1998), but a reduction in immunity has not been documented directly with drought conditions. One consequence, global warming, as frequency and severity of drought increases, may be increased vulnerability of populations to disease accompanied by more frequent disease epidemics (Epstein 2001; Harvell et al. 2002; Møller and Erritzøe 2003; Shaman et al. 2003, 2005). Rising temperatures could expand the distribution of vector-borne pathogens transmitted by arthropods, including mosquitoes, sand flies, midges, and ticks (Shope 1992, Epstein and Defilippo 2001, Shaman et al. 2005); many arthropod-borne disease epidemics are associated with droughts (Epstein and Defilippo 2001).

The drought of 2000–2002 in the southwestern United States, although not unprecedented (Allen and Breshears 1998), was one of the most severe in 50 years. We assessed cell-mediated immune response from 1997 to 2002 using a phytohaemagglutinin (PHA) injection in nestlings of three species of cavity-nesting birds: Ash-throated Flycatcher (*Myiarchus cinerascens*), Western Bluebird (*Sialia mexicana*), and Violet–green Swallow (*Tachycineta thalassina*). PHA response has been associated with body condition and survival (Hõrak et al. 1999, Alonso-Alvarez and Tella 2001). PHA injected for localized *in vivo* inflammatory response in birds has long been used to measure cell-mediated immunity (Stadecker et al. 1977, Lamont and Smyth 1984) and has been found to not impose additional stress or survival costs (Merino et al. 1999, Smits and Williams 1999). PHA has been shown to increase energy expenditure and food intake (Martin et al. 2003, Barbosa and Moreno 2004). Martin et al. (2006) found that PHA-induced swelling is related to heightened immune cell activity in House Sparrows (*Passer domesticus*) and that PHA-induced swelling is a tradeoff with other physiological functions.

Cell-mediated immunity is particularly important during the breeding season, because the likelihood of injury during sexual competition is high and cell-mediated immunity is essential for healing wounds and resisting infection (Zuk and Johnsen 1998). Our objectives were to: (1) compare three similar species in relation to nestling cell-mediated immune response, condition, and survival; and (2) examine the effects of severe drought on both nestlings and adults during the breeding season.

METHODS

Study Area.—This study was conducted at Los Alamos National Laboratory (LANL) in

[1] Los Alamos National Laboratory, Atmospheric, Climate, and Environmental Dynamics, MS J495, Los Alamos, NM 87545, USA.

[2] Corresponding author; e-mail: jmfair@lanl.gov

north-central New Mexico. The 111-km^2 facility is on the Pajarito Plateau and consists of a series of relatively narrow mesas separated by deep, steep-sided canyons that extend west to east-southeast along an elevation gradient from the Jemez Mountains to the Rio Grande. Vegetation community types range from open ponderosa pine (*Pinus ponderosa*) forest to piñon-juniper (*P. edulis*, *Juniperus osteosperma*) woodland. We placed 433 bluebird boxes on LANL property during winter 1997. Nest boxes were placed ~2 m above ground level on trees and spaced ~50–75 m apart.

All nest boxes were visited every 2 weeks starting in May 1997; nests with eggs were considered active and visited every 2 days until the first eggs hatched (day = 0). Nests were visited again on days 3, 10, 15 and 16. Ten percent of the Western Bluebird pairs had second broods, which did not differ between years and were not included in the analysis. All nests included in the analysis were new pairs not previously in the study. Each nestling was handled for <8 min/visit in accordance with the Guidelines for the Use of Wild Birds in Research (Gaunt and Oring 1997).

Measurements.—All nestlings in selected nests were injected intradermally on day 15 in the wing-web with either 0.05 ml (1.0 mg/ml) PHA in phosphate-buffered saline (PBS) (right side) or 0.05 ml PBS only (left side). This date was chosen, as it was latest date before fledging when this could be completed. The amount of swelling in the wing-web 24 hrs after inoculation was measured with a pocket dial gauge micrometer (L.S. Starrett® #1010, Athol, MA, USA) to the nearest 0.001 mm by the same person. The lower variance within individuals for PHA measurements using the left wings of Western Bluebirds and Ash-throated Flycatchers in 2002 with wing webs not injected with PBS (post 24 hrs) was derived from a one-way ANOVA using the GLM (general linear model) in SAS (SAS Institute 1998). Our estimates of individual variance, consistent with Lessells and Boag (1987), used the correlation coefficient calculated using the variance component of the data set. The variability of measuring PHA with just one observer was estimated to be 0.94 and associated $F_{1,81}$ ratio of 1127. A PHA index (Fair et al. 1999) to compare species was computed as the thickness of the PHA-inoculated wing-web minus the thickness of the opposite wing-web and standardized by the average wing thickness before inoculation. All PHA measurements were made by one person (JMF).

Nestlings were weighed at 15 days and survival of 864 nestlings was calculated up to the maximum of 14 days of age after hatching over 6 years. The length of the right ninth primary was measured with a ruler to the nearest mm using the flattened wing method (Svensson 1984). The left and right tarsi were measured with digital calipers to the nearest 0.1 mm. All birds were weighed using a digital balance to the nearest 0.01 g. Predation was relatively low with most known dead birds being found in the nest (Fair et al. 2003).

Probability of fledging for all three species after 14 days was 68% for all years combined. PHA-induced wing web swelling was measured for 225 Western Bluebird (WEBL), 40 Ash-throated Flycatcher (ATFL), and 33 Violet-green Swallow (VGSW) chicks. The majority of the flycatchers and swallows were measured for PHA in 2001 and 2002. Three hundred flycatchers were additionally measured for morphological parameters. Approximately 70-µl of blood was collected on day 15 of age from the brachial vein of the wing in heparinized microcapillary tubes, which were kept in a cooler. Heparinized capillary tubes were spun for 10 min in a micro-capillary centrifuge within 1 hr of collection. Hematocrit estimates from the blood collected were obtained directly using a microhematocrit reader.

Data Analysis.—We used SAS statistical software (SAS Institute 1987) for all analyses. PHA measurements were heteroscedastic between years ($F = 5.50$, $P < 0.0003$, Levene's Test), the data within nests were not independent, and we used the means of the PHA measurements for each nest in a nonparametric Kruskal-Wallis Test. Weight data were also not independent but had similar variances between years and we used a mixed general linear model (PROC MIXED). The nest box was included as a random factor to account for non-independence among young within a brood and fixed factors included nestling variables of body mass, species, and year. Comparisons of bluebird and flycatcher nestling

survival rates were analyzed using the log-rank procedure LIFETEST (SAS Institute 1987), which allows for right censoring of data points where the failure times to the right are missing. The log-rank procedure LIFETEST computes nonparametric estimates of the survivor function and rank tests for association of the response variable with other variables; it is more robust than the Wilcoxon statistic in detecting differences between groups.

RESULTS

Precipitation for this region was 25% below average during 2000 and 2001 and 65% below average through summer (Aug 2002). All three species had a similar reduction in the PHA-induced wing-web swelling response in 2001 and a more pronounced reduction in 2002 compared to the first 3 years of the study (WEBL, $\chi^2 = 40.3$ df = 4, $P < 0.0001$; ATFL, $\chi^2 = 10.2$, df = 3, $P = 0.0002$; VGSW, $\chi^2 = 13.4$, df = 1, $P = 0.0003$, Kruskal-Wallis) (Fig 1A). Response to PHA increased with annual precipitation for all three species (WEBL [$n = 225$], $r_s = 0.23$, $P = 0.003$; ATFL [$n = 40$], $r_s = 0.73$, $P < 0.001$; VGSW [$n = 33$, 2 yrs] $r_s = 0.42$, $P = 0.01$, Pearson Rank Correlation) (Fig. 1B). Western Bluebird and Ash-throated Flycatcher did not differ in response to PHA for the first 3 years of the study. However, Western Bluebird had a higher response in 2001 and 2002 to PHA than Ash-throated Flycatcher and Violet-green Swallow ($\chi^2 = 8.8$, df = 2, $P = 0.01$; $\chi^2 = 14.3$, df = 2, $P = 0.0008$), respectively. PHA response was not related to clutch size in any of the three species for any year except for Western Bluebird where birds with smaller clutch sizes (2 and 3) had lower responses to PHA than those with larger clutches (4 and 5) ($\chi^2 = 3.7$, df = 1, $P = 0.05$). One hundred and thirty-four birds received an antigenic challenge when they were 5 days of age; we tested for the any correlations between PHA response and the three antigens and control, and found no relationship ($F = 0.98$, df = 4 and 133, $P = 0.43$). This was not a confounding factor in the analysis.

Nestling body mass (g) was reduced for flycatcher and bluebird nestlings which weighed less in 2002 compared to all other years ($F = 18.02$, df = 3 and 36, $P < 0.0001$ $F = 31.02$, df = 4 and 220, $P < 0.0001$, respectively). The average body mass for Ash-throated Flycatcher was significantly lower in 2002 than all other years (LSD test) and was significantly lower for Western Bluebird in both 2001 and 2002 than in other years. Violet-green Swallows did not have previous years for comparison of body mass. Similarly, the right wing length of the ninth primary was significantly shorter in 2001 and 2002 for Western Bluebird ($F = 14.3$, df = 4 and 220, $P < 0.0001$), Ash-throated Flycatcher ($F = 12.1$, df = 4 and 87, $P < 0.0001$) and, in 2002, for Violet-green Swallow ($F = 7.5$, df = 1 and 31, $P < 0.01$). Length of the right tarsus did not differ between any years for Western Bluebird ($F = 0.62$, df = 4 and 220, $P < 0.0001$).

Survival to fledging age was not lower in 2002 ($\chi^2 = 54.3$, df = 5, $P < 0.0001$, log rank test) than in the previous 2 years, but was lower overall during the drought years of 2000–2002 compared to the first 3 years of the study (Fig. 2). Percent of eggs that hatched per clutch did vary between years for Western Bluebird with a reduced clutch size in 2002 from all other years ($F = 12.86$, df = 5 and 632, $P < 0.0001$). This was also similar for Ash-throated Flycatcher ($F = 10.38$, df = 5 and 223, $P < 0.0001$) and for Violet-green Swallow in 2002 ($F = 5.47$, df = 2 and 26, $P = 0.01$). Average clutch size for all three species was reduced by 21% in 2002. There was variation in hematocrit between years ($F = 3.32$, df = 5 and 128, $P = 0.007$) in adult Western Bluebirds that were captured, bled and banded ($n = 133$); but there was no clear pattern for year differences. There was also variability in mass (g) for adult bluebirds between years (2002, $\bar{x} \pm SE = 23.9 \pm 0.87$ g; other years 25.8 ± 0.44 g) with adults captured in 2002 weighing 7% less than in all previous years ($F = 4.50$, df = 5 and 112, $P = 0.0009$).

DISCUSSION

There was a dramatic decrease in the PHA-induced wing-web swelling in nestlings associated with unusually dry conditions. Adult Western Bluebirds captured in 2002 weighed 7% less than in all previous years. Average body mass was also reduced for flycatcher and bluebird nestlings, which weighed less in

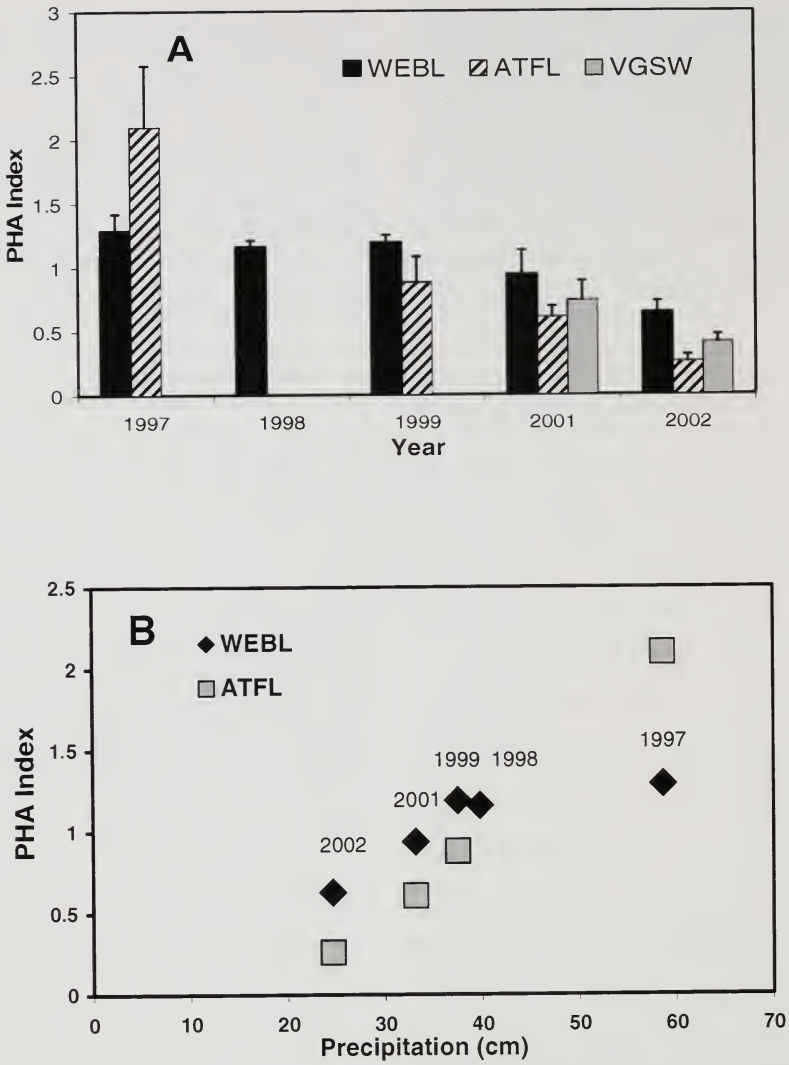


FIG. 1. (A). Cell-mediated response to PHA was significantly reduced in 2002 from all other years (PHA index [mean ± SE]). Morphological and immune data were not collected during 2000 due a large-scale fire adjacent to the study area in May 2000. (B). Cell-mediated response to PHA for annual average precipitation from 1997 to 2002.

2002 compared to all other years, indicating nutritional stress was potentially related to drought conditions. Survival to fledging age in Western Bluebird nestlings was not lower in 2002 than in the previous 2 years, but was lower overall during the drought years of 2000–2002 compared to the first 3 years of the study (Table 1). Hematocrit did not provide additional information on impacts of drought on condition due to variability between individuals and years.

There is no direct published evidence for effects of drought on cell-mediated response, but numerous studies document the cell-mediated immune function is strongly correlated with nestling body mass (Saino et al. 1997, Christe et al. 1998, Tella et al. 2001, Westneat et al. 2004), availability and quality of food (Lochmiller et al. 1993, Birkhead et al. 1998, Gonzales et al. 1999, Hoi-Leitner et al. 2001, Lifjeld et al. 2002) and the overall environment (Brinkhof et al. 1999, Tella et al. 2000). Lifjeld et al. (2002) found that cell-mediated immune response is affected by weather con-

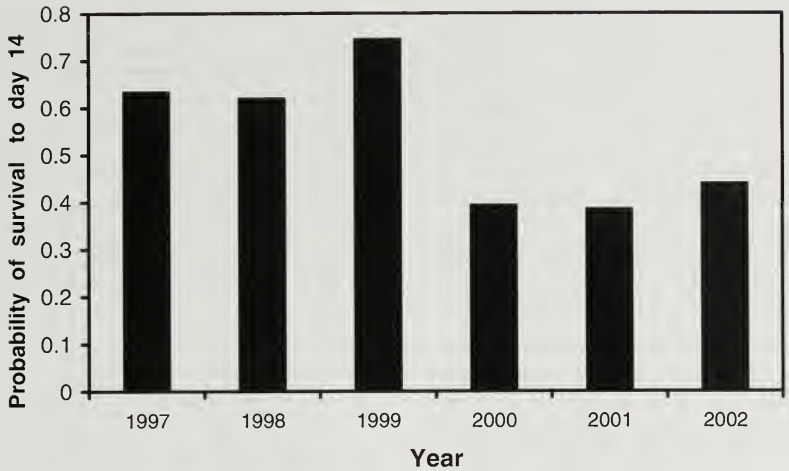


FIG. 2. Probability of nestling survival to day 14, before fledging, for 1997–2002.

ditions in particular, and that PHA response is influenced by short-term fluctuations in energy balance. The PHA response in this study was measured over the entire summer and the measurements should include daily variation during the breeding season. We demonstrate wide variation in PHA between years that coincides with a significant drought, but do not have food limitation data to identify the exact relationship. It is also not clearly understood how much variation in PHA response is heritable, as there has been conflicting evidence (Brinkhof et al. 1999, Tella et al. 2000, Martin et al. 2006). Other environment conditions such as increased exposure to predators have also been shown to decrease the avian cell-mediated response (Navarro et al. 2004).

The mostly likely mechanism for reduction in cell-mediated immune response, reduced weight, and nestling survival would be food availability and parental effort. There has been relatively little research documenting impacts of drought on arthropod communities, but one study experimentally showed that drought negatively impacted farmland arthropod communities (Frampton et al. 2000). Studies on the impacts of drought on arthropods or other prey in relation to parental effort and development would help in understanding the exact mechanism involved in impacts of severe drought on birds and immune function.

One of our most significant findings was that clutch size for all three species was reduced by 21% in 2002—a result that follows

TABLE 1. Average individual and nest characteristics for three cavity-nesting species for 1997–1999 (average precipitation) and 2000–2002 (below average precipitation).

Species and year	Body mass, g	Tarsus length, mm	Survival to day 14, %	PHA Index (*n*)	Clutch size	Hatch date	Percent hatch	Number of individuals for PHA	Number of nests
Ash-throated Flycatcher									
1997–1999	25.6	26.3	50.7	1.7 (10)	3.9	175.8	75.7	10	53
2000–2002	25.2	25.5	23.0	0.51 (20)	3.4	170.8	67.1	30	50
Violet-green Swallow									
1997–1999									
2000–2002	17.5	13.6	44.8	0.51 (33)	3.3	183.3	70.2	33	30
Western Bluebird									
1997–1999	26.5	23.0	74.5	1.2 (197)	4.5	165.4	70.6	197	170
2000–2002	22.7	22.8	53.2	0.76 (28)	4.1	164.2	72.8	28	90

Tella et al. (2000) who found that cell-mediated immune response was higher in nestlings from larger clutches. However, this does not follow the studies of Hõrak et al. (1999) and Ilmonen et al. (2003) who found an increase in brood size reduced the cell-mediated immune response. We found no relationship between timing of breeding during the season (hatch date) and response to PHA. Many of the tradeoffs between brood size, development, parental effort, and food availability remain to be understood, but the impact of extreme environmental conditions can be measured in immune function. Martin et al. (2006) noted that PHA-induced swelling does not appear to be an unambiguous index of T-cell-mediated immunity, but rather a multifaceted index of cutaneous immune activity that may be affected by the physiological state of the individual as well as the life-history traits of the species. Our study documents a decrease in PHA-induced swelling over several years on the same day of nestling development within the same species that is associated with a reduction in precipitation and nestling mass and survival.

ACKNOWLEDGMENTS

We thank P. C. Beeson, K. F. Colestock, L. A. Haussamen, Tina Sommer, and C. E. Talus for excellence in field assistance. We thank C. D. Allen, D. B. Breshears, M. H. Ebinger, H. A. Hinojosa, J. M. Heikoop, L. K. Marsh, P. M. Rich, and R. E. Ricklefs for comments on an earlier draft. We also thank B. K. Sandercock for helpful comments on the manuscript. We thank O. B. Myers for initiation of the nest box-monitoring network. The animal care and use committees of both LANL and the University of Missouri-St. Louis approved all protocols. This research was funded by the Environmental Restoration Program through Los Alamos National Security LLC, operator of the Los Alamos National Laboratory under Contract DE-AC52-06NA25396 with the U.S. Department of Energy.

LITERATURE CITED

Allen, C. and D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences of the USA. 95:14839–14842.

Alonso-Alvarez, C. and J. Tella. 2001. Effects of experimental food restriction and body mass changes on the avian T-cell-mediated immune response. Canadian Journal of Zoology 79:101–105.

Apanius, V. 1998. Stress and immune response. Pages 133–153 *in* Advances in the study of behavior. Volume 27. Stress and behavior (A. P. Møller, M. Milinski, and P. Slater, Editors). Academic Press, San Diego, California, USA.

Barbosa, A. and E. Moreno. 2004. Cell-mediated immune response affects food intake but not body mass: an experiment with wintering Great Tits. Ecoscience 11:305–309.

Birkhead, T., F. Fletcher, and E. Pellat. 1998. Sexual selection in the Zebra Finch (*Taeniopygia guttata*): condition, sex traits and immune capacity. Behavioral Ecology and Sociobiology 44:179–191.

Brinkhof, M. W., P. Heeb, M. Kölliker, and H. Richner. 1999. Immunocompetence of nestling Great Tits in relation to rearing environment and parentage. Proceedings of the Royal Society of London, Series B 266:2315–2322.

Christe, P., A. P. Møller, and F. de Lope. 1998. Immunocompetence and nestling survival in the House Martin: the tasty chick hypothesis. Oikos 83:175–179.

Epstein, P. 2001. Climate change and emerging infectious diseases. Microbes and Infection 3:747–754.

Epstein, P. and J. Defilippo. 2001. West Nile virus and drought. Global Change and Human Health 2: 105–107.

Fair, J. M., E. Hansen, and R. E. Ricklefs. 1999. Growth, developmental stability and immune response in juvenile Japanese Quail. Proceedings of the Royal Society of London, Series B 266:1735–1742.

Fair, J. M., O. B. Myers, and R. E. Ricklefs. 2003. Immune and growth response of Western Bluebirds and Ash-throated Flycatchers to soil contaminants. Ecological Applications 13:1817–1829.

Frampton, G. K., P. J. van den Brink, and P. J. L. Gould. 2000. Effects of spring drought and irrigation on farmland arthropods in southern Britain. Journal of Applied Ecology 37:865–883.

Gaunt, A. and L. Oring. 1997. Guidelines to the use of wild birds in research. The Ornithological Council, Washington, D.C., USA.

George, T., A. Fowler, R. Knight, and L. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275–284.

Gonzales, G., G. Sorci, A. P. Møller, P. Ninni, C. Haussy, and F. de Lope. 1999. Immunocompetence and condition-dependent sexual advertisement in male House Sparrows (*Passer domesticus*). Journal of Animal Ecology 68:1225–1234.

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296: 2158–2162.

Hoi-Leitner, M., M. Romero-Pujante, H. Hoi, and A. Pavlova. 2001. Food availability and immune capacity in Serin (*Serinus serinus*) nestlings. Behavioral Ecology and Sociobiology 49:333–339.

Hõrak, P., L. Tegelmann, I. Ots, and A. P. Møller. 1999. Immune function and survival of Great Tit nestlings in relation to growth conditions. Oecologia 121:316–322.

Ilmonen, P., D. Hasselquist, Å. Langefors, and J. Wiehn. 2003. Stress, immunocompetence and leukocyte profiles of Pied Flycatchers in relation to brood size manipulation. Oecologia 136:148–154.

Lamont, S. and J. Smyth. 1984. Effect of selection for delayed amelanosis on immune response in chickens. 2. Cell-mediated immunity. Poultry Science 63:440–442.

Lessells, C. M. and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Lifjeld, J., P. Dunn, and L. Whittingham. 2002. Short-term fluctuations in cellular immunity of Tree Swallows feeding nestlings. Oecologia 130: 185–190.

Lochmiller, R. L., M. R. Vestey, and J. C. Boren. 1993. Relationship between protein nutritional status and immunocompetence in Northern Bobwhite chicks. Auk 110:503–510.

Martin, L. B., A. Scheuerlein, and M. Wikelski. 2003. Immune activity elevated energy expenditure of House Sparrows: a link between direct and indirect costs? Proceedings of the Royal Society of London, Series B 270:153–158.

Martin II, L. B., P. Han, J. Lewittes, J. R. Kuhlman, K. C. Klasing, and M. Wikelski. 2006. Phytohemagglutinin-induced skin swelling in birds: histological support for a classic immunoecological technique. Functional Ecology 20:290–299.

Merino, S., J. Martínez, A. P. Møller, S. Sanabria, F. de Lope, J. Pérez, and F. Rodriguez-Caabeiro. 1999. Phytohaemagglutinin injection assay and physiological stress in nestling House Martins. Animal Behavior 58:219–222.

Møller, A. P. and J. Erritzøe. 2003. Climate, body condition, and spleen size in birds. Oecologia 137: 621–626.

Navarro, C., F. de Lope, A. Marzal, and A. Møller. 2004. Predation risk, host immune response, and parasitism. Behavioral Ecology 15:629–635.

Saino, N., S. Calza, and A. Møller. 1997. Immunocompetence of nestling Barn Swallows in relation to brood size and parental effort. Journal of Animal Ecology 66:827–836.

SAS Institute Inc. 1987. SAS/STAT guide for personal computers. Sixth Edition. SAS Institute Inc., Cary, North Carolina, USA.

Shaman, J., J. F. Day, and M. Stieglitz. 2003. St. Louis encephalitis virus in wild birds during the 1990 south Florida epidemic: the importance of drought, wetting conditions, and the emergence of *Culex nigripalpus* (Diptera: Culicidae) to arboviral application and transmission. Journal of Medical Entomology 40:547–554.

Shaman, J., J. F. Day, and M. Stieglitz. 2005. Drought-induced amplification and epidemic transmission of West Nile virus in southern Florida. Journal of Medical Entomology 42:134–141.

Shope, R. E. 1992. Impacts of global climate change on human health: spread of infectious disease. Pages 363–70 *in* Global climate change: implications, challenges and mitigation measures (S. K. Majumdar, L. S. Kalkstein, B. Yarnal, E. W. Miller, and L. M. Rosenfeld, Editors). The Pennsylvania Academy of Science, Easton, USA.

Smits, J. and T. Williams. 1999. Validation of the immunotoxicology techniques in passerine chicks exposed to oil sand tailings water. Ecotoxicology and Environmental Safety 44:105–112.

Stadecker, M., M. Lukic, A. Dvorak, and S. Leaskowitz. 1977. The cutaneous basophil response to phytohemagglutinin in chickens. Journal of Immunology 118:1564–1568.

Svensson, L. 1984. Identification guide to European passerines. Second Edition. Stockholm and British Trust for Ornithology, Thetford, United Kingdom.

Tella, J. L., G. Bortolotti, M. G. Forero, and R. Dawson. 2000. Environmental and genetic variation in T-cell-mediated immune response of fledgling American Kestrels. Oecologia 123:453–459.

Tella, J. L., M. G. Forero, G. Bortolotti, J. A. Donázar, G. Blanco, and O. Cellallos. 2001. Offspring body condition and immunocompetence are negatively affected by high breeding densities in colonial seabirds: a multiscale approach. Proceedings of the Royal Society of London, Series B 268:1455–1461.

Westneat, D., J. Weiskittle, R. Endenfield, T. Kinnard, and J. Poston. 2004. Correlates of cell-mediated immunity in nestling House Sparrows. Oecologia 141:17–23.

Zuk, M. and T. Johnsen. 1998. Seasonal changes in the relationship between ornamentation and immune response in Red Jungle Fowl. Proceedings of the Royal Society of London, Series B 265: 1631–1635.

The Wilson Journal of Ornithology 120(4):820–829, 2008

INFLUENCE OF GRAZING AND AVAILABLE MOISTURE ON BREEDING DENSITIES OF GRASSLAND BIRDS IN THE CENTRAL PLATTE RIVER VALLEY, NEBRASKA

DANIEL H. KIM,[1,4] WESLEY E. NEWTON,[2] GARY R. LINGLE,[1,3] AND FELIPE CHAVEZ-RAMIREZ[1]

ABSTRACT.—We investigated the relationship between grassland breeding bird densities and both grazing and available moisture in the central Platte River Valley, Nebraska between 1980 and 1996. We also compared species richness and community similarity of breeding birds in sedge (*Carex* spp.) meadows and mesic grasslands. Densities of two species had a significant relationship with grazing and six of seven focal species had a significant relationship with available moisture. Bobolink (*Dolichonyx oryzivorus*) and Brown-headed Cowbird (*Molothrus ater*) densities were lower in grazed plots compared to ungrazed plots, whereas Red-winged Blackbird (*Agelaius phoeniceus*) densities were greater in sedge-meadow plots compared to mesic grassland plots. Bobolink, Dickcissel (*Spiza americana*), and Brown-headed Cowbird were negatively associated with available moisture with breeding densities peaking during the driest conditions. Our results suggest that wet conditions increase species richness for the community through addition of wetland-dependant and wetland-associated birds, but decrease densities of ground-nesting grassland birds in wet-meadow habitats, whereas dry conditions reduce species richness but increase the density of the avian assemblage. We propose that wet-meadow habitats serve as local refugia for grassland-nesting birds during local or regional droughts. *Received 9 October 2007. Accepted 21 March 2008.*

Grassland birds have experienced greater population declines over the past 40 years than any other avian group in North America (Askins 1993, Sauer et al. 2005). These declines in the Midwest and Great Plains have been attributed to loss of grasslands in breeding areas (Knopf 1994, Herkert 1995). Many recent studies of grassland birds have examined the effects of habitat loss and fragmentation on avian occurrence and abundance (e.g., Herkert et al. 2003). Several studies also have examined the impacts of natural ecological drivers, such as burning and grazing, but only a few studies have evaluated the dynamic wet-dry cycles associated with grasslands and their influence on avian densities or nest success (Cody 1985, George et al. 1992, Zimmerman 1992, Igl and Johnson 1999, Fuhlendorf et al. 2006).

The dominant historical ecological factors were fire and grazing in the eastern mesic tallgrass prairies (Steinauer and Collins 1996), while the historical ecological drivers in the shortgrass prairies in the western Great Plains were climate and grazing (Bragg and Steuter 1996). The mixed-grass prairie ecosystem represents the integration of the characteristics of the tallgrass and shortgrass prairies as influenced by climate and soils (Bragg and Steuter 1996). As the climate becomes more arid from the eastern tallgrass prairies to the western shortgrass plains, drought supersedes fire as the primary ecological factor.

Vegetation structure may be the most important aspect of habitat selection and suitability for grassland birds (Wiens 1969, 1973; Cody 1981; George et al. 1992; Winter et al. 2005). The forb component in mixed-grass systems, which is responsible for the majority of the structural variation, is directly affected by precipitation (Bragg and Steuter 1996). Grassland bird populations respond quickly to and are relatively tolerant of changes in vegetation structure resulting from natural (e.g., drought, wildfire) and anthropogenic disturbances (e.g., mowing, prescribed fire) (Dechant et al. 2003a, b, c; Herkert 2003). In addition, fluctuations in precipitation affect food resource availability through reductions in insect biomass during drought years (Wittenberger 1980, George et al. 1992).

[1] Platte River Whooping Crane Maintenance Trust Inc., 6611 West Whooping Crane Drive, Wood River, NE 68883, USA.

[2] U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th Street SE, Jamestown, ND 58401, USA.

[3] Current Address: Aim Consulting, 1568 L Road, Minden, NE 68959, USA.

[4] Corresponding author; e-mail: Dkim@whoopingcrane.org

Vegetation structure within the Platte River Valley of south-central Nebraska is influenced by both vegetation association and management practices. Vegetation associations in riparian wet-meadow pastures in this region vary from wetland emergent vegetation to dry-ridge grasslands based on elevation above the water table (Henszey et al. 2004). Sedge (*Carex* spp.) meadows and mesic tallgrass prairies are the dominant plant communities in native and restored areas within the riparian corridor and provide patches of suitable habitat for grassland birds in a mosaic of crop fields with strips of gallery forests.

We evaluated the influence of grazing and available moisture on breeding densities of grassland birds in mesic prairies and sedge meadows. We had two major objectives: (1) document differences in avian assemblages between sedge-meadow and mesic prairie plots using community metrics (richness and similarity), and (2) examine the impacts of grazing and fluctuating wet-dry cycles on the density of seven grassland bird species.

TABLE 1. Study design and classification of Palmer Drought Severity Index (PDSI) into five categories. Grazing treatments included grazing (1) and no grazing (0). No data (ND) were collected in 1991 and 1992 or in sedge plot 4 in 1981.

Year	PDSI (Aug)	PDSI category (midpoint)	Mesic plots		Sedge plots	
			1	2	3	4
1980	−1.89	A (−0.91)	1	1	1	1
1981	1.42	B (1.06)	1[a]	0	1	ND
1982	2.54	C (3.03)	0	0	0	1
1983	3.74	C (3.03)	1	0[a]	1[a]	1
1984	4.59	D (4.99)	1[a]	1[a]	0	1
1985	4.20	D (4.99)	1[a]	0[a]	0	1
1986	3.24	C (3.03)	0	0[a]	0	1
1987	4.10	D (4.99)	0[a]	0	0[a]	1
1988	1.64	B (1.06)	0	1[a]	0[a]	1[a]
1989	0.60	B (1.06)	1	0	0[a]	1[a]
1990	0.54	B (1.06)	0	1	0	0
1991	ND	ND	ND	ND	ND	ND
1992	ND	ND	ND	ND	ND	ND
1993	7.94	E (6.96)	1	0	0	1
1994	4.23	D (4.99)	0[a]	1	0	0[a]
1995	−0.59	A (−0.91)	0	0[a]	0	0
1996	2.21	C (3.03)	0	1[a]	0	0

[a] Indicates that plot was burned during spring. Most prescribed fire resulted in patchy burns resulting in no detectable affects of fire to species density in this study.

METHODS

Study Area and Management.—Research occurred on lands owned and managed by the Platte River Whooping Crane Maintenance Trust Inc. (hereafter "the Trust"). The Trust owns and manages >4,000 ha of cropland, wet-meadow grasslands, and gallery forests in Hall, Buffalo, and Phelps counties along the Platte River in central Nebraska. The study area was Mormon Island Crane Meadows in Hall County, Nebraska (40° 48′ N, 98° 26′ W). Wet meadows were managed using a three-pasture grazing rotation. Each pasture was grazed either in the early season (May–late Jun), mid season (late Jun–mid Aug) or late season (mid Aug–mid Oct). Rotation order changed annually (Table 1), and management included periodic prescribed burns to discourage woody plant encroachment (Currier et al. 1985). We categorized pastures as grazed only if cattle were present in the early grazing season (i.e., before or during the bird censuses).

Four permanent 16-ha plots were established on Mormon Island Crane Meadows (MICM) in Hall County, Nebraska and classified as either sedge meadow or mesic prairie following recommendations of Henszey et al. (2004). Plots 1 and 2 were classified as mesic prairie and had greater topographic relief, raising them above the water table and resulting in greater densities of goldenrod (*Solidago* spp.), Maximilian sunflower (*Helianthus maximiliani*), and yellow sweetclover (*Melilotus officinalis*). Plots 3 and 4 were classified as sedge meadow, were 15–60 cm closer to the water table, and included expansive seasonal wetland habitat. Plots 3 and 4 were characterized by intermittent relic channels dominated by aquatic sedge (*Carex aquatilis*), which formed hummocks as a result of grazing and the presence of indigo bush (*Amorpha fruticosa*) near sloughs and relic channels. All plots occurred within the largest contiguous tract (>1,000 ha) of wet-meadow habitat in the central Platte River Valley (Lingle 1981). Spatially, no plot was further than 2.0 km from any other plot and all plots occurred within the same landscape. The plots do not represent true replicates, but they were on different grazing schedules.

Palmer Drought Severity Index.—We downloaded Palmer Drought Severity Index (PDSI) data for central Nebraska (State Cli-

TABLE 2. Densities (males/10 ha) of species detected during breeding bird censuses at Mormon Island Crane Meadows in Hall County, Nebraska, 1980-1996. Densities are by plot and averaged across years. Plots 1 and 2 represent mesic mixed-grass prairie, and plots 3 and 4 represent sedge-meadow grasslands.

Species	Plot 1	Plot 2	Plot 3	Plot 4
Least Bittern (*Ixobrychus exilis*)	0.000	0.000	0.042	0.021
Wood Duck (*Aix sponsa*)	0.000	0.000	0.000	0.021
Mallard (*Anas platyrhynchos*)	0.000	0.000	0.250	0.417
Northern Pintail (*A. acuta*)	0.000	0.000	0.000	0.000
Blue-winged Teal (*A. discors*)	0.125	0.042	0.323	0.313
Virginia Rail (*Rallus limicola*)	0.000	0.000	0.000	0.042
Ring-necked Pheasant (*Phasianus colchicus*)	0.042	0.000	0.000	0.000
Northern Bobwhite (*Colinus virginianus*)	0.021	0.042	0.000	0.000
Killdeer (*Charadrius vociferous*)	0.229	0.000	0.313	0.477
Upland Sandpiper (*Bartramia longicauda*)	1.615	1.500	1.302	1.208
Wilson's Snipe (*Gallinago delicata*)	0.000	0.000	0.063	0.042
Wilson's Phalarope (*Phalaropus tricolor*)	0.000	0.000	0.438	0.813
Mourning Dove (*Zenaida macroura*)	0.094	0.125	0.198	0.510
Sedge Wren (*Cistothorus platensis*)	0.208	0.000	0.146	0.271
Common Yellowthroat (*Geothlypis trichas*)	0.000	0.000	0.000	0.063
Grasshopper Sparrow (*Ammodramus savannarum*)	1.823	3.208	0.792	1.052
Swamp Sparrow (*Melospiza georgiana*)	0.000	0.000	0.000	0.083
Dickcissel (*Spiza americana*)	2.354	1.396	3.031	1.271
Bobolink (*Dolichonyx oryzivorus*)	5.313	4.938	5.677	4.969
Red-winged Blackbird (*Agelaius phoeniceus*)	1.333	0.167	7.323	7.208
Eastern Meadowlark (*Sturnella magna*)	0.083	0.167	0.083	0.021
Western Meadowlark (*S. neglecta*)	1.729	1.573	0.948	1.271
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	0.000	0.000	0.000	0.083
Brown-headed Cowbird (*Molothrus ater*)	1.917	1.542	2.563	2.625
Focal species density	16.083	14.323	21.640	19.604
Mean species richness	6.8	6.1	8.1	10.0
Species richness	14	11	16	21

mate Division 5) from the National Climate Data Center web site (http://www.ncdc.noaa.gov/oa/climate/research/monitoring.html). The PDSI is a long-term drought index calculated monthly and incorporates both precipitation and temperature data (Palmer 1965). The PDSI expresses the severity of a wet (positive values) or dry (negative values) period by factoring in both past and present conditions. More specifically, values of zero to −0.5 indicate normal moisture conditions, −0.5 to −1.0 indicate incipient drought, −1.0 to −2.0 indicate mild drought, −2.0 to −3.0 indicate moderate drought, −3.0 to −4.0 indicate severe drought, and less than −4.0 indicate extreme drought. Similar adjectives are associated with positive values and wet periods. Each state is divided into climate regions and PDSI values are calculated independently for each region. We evaluated the relationship between PDSI values from each month in the breeding season (May–Aug) and annual breeding bird abundances using simple correlation coefficients for each individual species and all focal species combined. PDSI values from August had the highest correlations with all species except Grasshopper Sparrow (scientific names of birds are in Table 2), which was more highly correlated with PDSI values from May. We used PDSI values from August for further evaluation of species response to climatic factors with August values representing cumulative conditions through the breeding season.

Avian Surveys.—We conducted spot map surveys on each of the four 16-ha wet-meadow plots following standard Breeding Bird Census techniques (Van Velzen 1972). We systematically walked each plot on a minimum of eight mornings during the breeding season. Each territorial male present, its behavior, and the location of all nests found were mapped. Only female Brown-headed Cowbirds were counted, except in 1980, when

they were present but not counted. Eight surveys for each plot were conducted annually between 0505 and 1059 hrs CST from 23 May to 25 June from 1980 to 1990, and from 1993 to 1996 for a total of 15 years of data on plots 1–3. Plot 4 had 14 years of data, because no data were collected in that plot in 1981. Annual reports for these study sites were published in *American Birds* and *Journal of Field Ornithology* (Hay and Lingle 1982; Lingle and Whitney 1983a, b; 1991a, b; Lingle and Haugh 1984a, b; Lingle and Bedell 1989a, b; 1990a, b; Lingle et al. 1994a, b; Lingle 1995a, b; 1996a, b).

Statistical Analyses.—We report species richness for each plot for all 15 years and averaged across years. We compared avian communities using Morisita's (1959) Similarity Index, which ranks community similarity from 0.0 (no species overlap) to 1.0 (complete overlap). We calculated densities for each species on each plot (males/10 ha). We selected seven focal species (Upland Sandpiper, Grasshopper Sparrow, Dickcissel, Bobolink, Red-winged Blackbird, Western Meadowlark, and Brown-headed Cowbird) that were either obligate grassland nesting birds or strongly associated with grassland habitats and which occurred consistently across all four plots.

We used analysis of variance (ANOVA) to assess the effects of PDSI and grazing on the density of each bird species and overall avian diversity. We considered the design structure to be in the form of a strip-plot (Milliken and Johnson 1984). Given that PDSI is completely aliased with year (i.e., regional PDSI values are unique to each year but the same for all plots within a year), we first placed PDSI values into five categories (0–20, 21–40, 41–60, 61–80, and 81–100 percentiles). We considered these five levels of PDSI to be applied across each of the four plots simultaneously as "strips" with grazing applied randomly within each plot by PDSI combination. The results of this categorization and randomization varied (Table 1) with midpoint values of each PDSI category indicating reasonable spread and randomness of each factor level across years. We considered each of the four plots as random blocks for each PDSI by grazing level combination. Multiple occurrences of each PDSI category by grazing level combination were considered as sub-samples in time (Steel and Torrie 1980). We used PROC MIXED (SAS Institute Inc. 2004) to conduct the ANOVAs by considering three error terms and by computing Type III sums-of-squares using the most appropriate *F*-tests based on expected mean squares (Littell et al. 2006). We used Fisher's protected LSD test for pairwise comparisons between means for significant main effects and interactions at $P = 0.05$ (Milliken and Johnson 1984). All means reported are least squares means (lsmeans) with standard errors. We performed a similar analysis for prescribed burns and PDSI, but no significant associations were found. Thus, we do not report means or statistics for burn effects.

RESULTS

Plot Similarity and Species Richness.—Species richness (s) was greater for sedge-meadow plots ($s = 18.5$) compared to mesic-grassland plots ($s = 12.5$) (Table 2). Mesic-prairie plots were more similar to each other ($C_\lambda = 0.83$) than to sedge-meadow plots ($0.72 > C_\lambda > 0.51$) using Morisita's Similarity Index (C_λ); however, sedge-meadow plots had the greatest similarity ($C_\lambda = 0.90$).

PDSI Values.—Moisture conditions varied over the 15 years of study from mild drought (PDSI = −1.89) to extremely wet (PDSI = 7.94, flooded fields with only patches of dry ground available for nesting). Many of the bird species commonly associated with wet meadows and wetlands were detected only during extremely wet or flood conditions. For example, Virginia Rail, Wilson's Snipe, and most waterfowl species were detected only on wet-meadow plots during relatively wet seasons (PDSI > 3.0).

Bird Densities.—ANOVA results indicated the main effects of grazing and available moisture (i.e., PDSI), and their interaction, varied for each focal species and for all focal species combined (Table 3, Fig. 1). Data for all focal species combined indicated a significant relationship with PDSI main effect but with no grazing or interaction effects. The densities for all focal species combined, averaged across PDSI levels, were similar between ungrazed plots (32.1 ± 4.00 males/10 ha) and grazed plots (28.5 ± 3.92 males/10 ha). The densities of all focal species combined, averaged across the two grazing re-

TABLE 3. Analysis of variance assessing effects of grazing and available moisture (Palmer Drought Severity Index) on species densities.

Species	Grazing[a] F_{df}-test[b]	PDSI F_{df}-test[b]	Interaction F_{df}-test[b]
Focal species	$F_{1,3} = 7.34$	$F_{4,8} = 30.52$**	$F_{4,8} = 0.13$
Upland Sandpiper	$F_{1,3} = 9.49$	$F_{4,8} = 9.31$**	$F_{4,8} = 5.59$*
Grasshopper Sparrow	$F_{1,3} = 3.56$	$F_{4,8} = 3.81$	$F_{4,8} = 3.18$
Dickcissel	$F_{1,3} = 0.03$	$F_{4,8} = 68.21$**	$F_{4,8} = 2.15$
Bobolink	$F_{1,3} = 15.33$*	$F_{4,8} = 8.82$**	$F_{4,8} = 1.51$
Red-winged Blackbird	$F_{1,3} = 0.73$	$F_{4,8} = 8.88$**	$F_{4,8} = 0.96$
Western Meadowlark	$F_{1,3} = 5.77$	$F_{4,8} = 32.15$**	$F_{4,8} = 3.82$
Brown-headed Cowbird	$F_{1,3} = 11.62$*	$F_{3,5} = 13.31$**	$F_{3,5} = 0.63$

[a] Grazed fields had cattle in the plots during spot mapping; fallow fields were not grazed during the census period.
[b] Significance level: * $P < 0.05$; ** $P < 0.01$.

gimes, declined with increasing PDSI from 41.9 ± 4.78 males/10 ha at the lowest level of PDSI (−0.91) to 14.0 ± 8.15 males/10 ha at the highest level of PDSI (6.96).

Bobolink and Brown-headed Cowbird densities indicated significant main effects for grazing and PDSI but no interaction between the two effects. Bobolink densities, averaged across all PDSI levels, were higher on ungrazed plots (11.5 ± 1.06 males/10 ha) than on grazed plots (5.3 ± 1.08 males/10 ha). Bobolink densities, averaged across the two grazing regimes, declined from 11.8 ± 1.15 males/10 ha at the lowest level of PDSI (−0.91) to 6.4 ± 1.50 males/10 ha at the highest level of PDSI (6.96). Brown-headed Cowbird patterns paralleled those of Bobolink. Densities were higher on ungrazed plots (4.3 ± 0.61 females/10 ha) than on grazed plots (2.6 ± 0.59 females/10 ha) and tended to decline with increasing levels of PDSI (3.9 ± 0.59 females/10 ha at PDSI 1.51 to 3.0 ± 0.99 females/10 ha at PDSI 6.96).

Upland Sandpiper had a significant grazing by PDSI interaction. Their densities on grazed plots were near constant with a mean of 2.9 ± 0.34 males/10 ha across the PDSI levels. Densities on ungrazed plots peaked at intermediate levels of PDSI (2.6 ± 0.99 males/10 ha) with low densities at both the lowest PDSI level (0.6 ± 0.58 males/10 ha) and at the highest PDSI level (0.0 ± 0.76 males/10 ha).

Dickcissel, Western Meadowlark, and Red-winged Blackbird densities varied significantly with PDSI with no indication of grazing main effects or grazing by PDSI interactions. Dickcissel densities declined with increasing PDSI levels when averaged across both grazing treatments from 5.9 ± 1.05 males/10 ha (PDSI -0.91) to 0.3 ± 1.60 males/10 ha (PDIS 6.96). Western Meadowlark densities were low (all <4.0 males/10 ha) with no significant interaction occurring between PDSI and grazing, but Western Meadowlark experienced the most erratic patterns in densities across PDSI levels. Western Meadowlark declined significantly across the PDSI levels from 2.8 ± 0.29 males/10 ha (PDSI −0.91) to 2.0 ± 0.53 males/10 ha (PDSI 6.96). Red-winged Blackbird densities varied significantly with PDSI but had no grazing effects; the species declined only slightly from 8.6 ± 3.30 males/10 ha to 5.2 ± 3.60 males/10 ha with increasing PDSI.

Grasshopper Sparrow had non-significant increases in densities under grazed treatments for the lowest PDSI level (−0.91), but had no difference between grazing treatments or across PDSI levels. Grasshopper Sparrow mean density was 2.76 ± 0.37 males/10 ha across all levels of PDSI and the two grazing treatments.

DISCUSSION

All study plots were in close proximity, but small variations in elevation (at the decimeter scale) influenced the vegetative communities (Henszey et al. 2004) and, concomitantly, avian communities. Sedge-meadow pastures had a higher water table and were more susceptible to flooding. Thus, sedge-meadow plots had greater species richness due to wetland-associated and -dependant bird species using inundated fields during wet periods (Table 1). The extent of inundation depended on both local precipitation and river flood stage; in

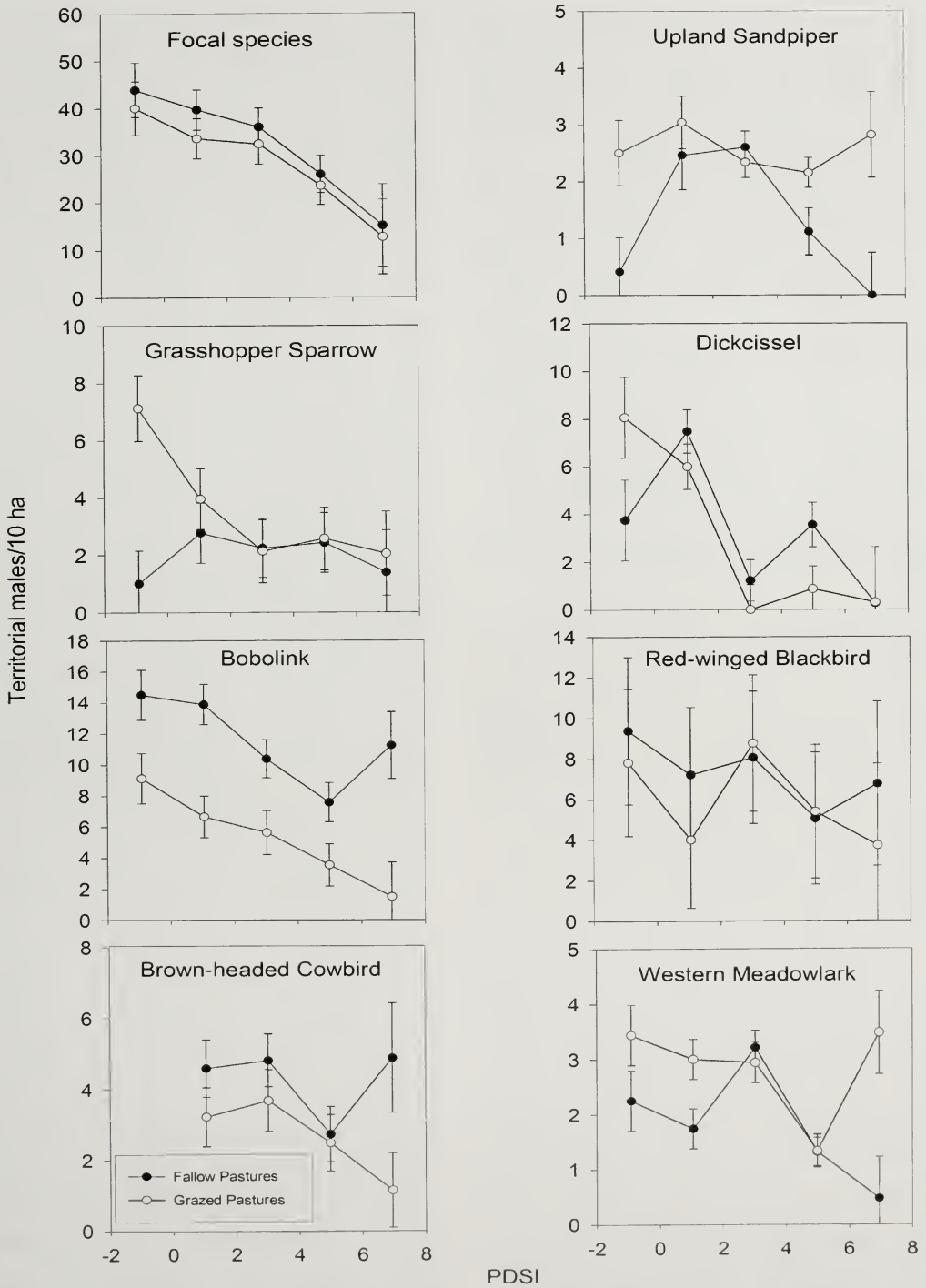


FIG. 1. Effects of moisture availability (Palmer Drought Severity Index or PDSI) on density of grassland birds. Open circles represent grazed plots, and closed circles represent ungrazed plots. The PDSI ranges from −2 (drier than normal, minimal standing water) to 8 (very wet, plots flooded).

some years, inundation may result from upstream releases from reservoirs on the Platte River rather than local precipitation patterns.

The Bobolink's predilection for ungrazed pastures is supported by findings from other studies (Bollinger 1995, Fritcher et al. 2004, Winter et al. 2005), and likely reflects this species' preference for moderate to tall, dense vegetation (Dechant et al. 2003b). The negative relationship between Bobolink densities and PDSI suggests that nest sites may be limited during wet years or there are moisture-related movements of Bobolink between riparian and upland grasslands. Some studies of banded Bobolink populations noted site fidelity increases with habitat quality in stable environments (Bollinger and Gavin 1989, Fletcher et al. 2006). Grazing and climatic fluctuations might remove predictability from riparian grasslands at our study sites, potentially facilitating movements at the patch scale.

We did not find a strong relationship between grazing and densities of Grasshopper Sparrow, Western Meadowlark, and Upland Sandpiper. Previous studies have reported these three species breed in actively managed (burned, grazed or hayed) grasslands (Dechant et al. 1999, 2003a, d), but the low overall densities for all three species limited the statistical power to detect a strong grazing-treatment effect. Upland Sandpipers typically are associated with early seral stages in grasslands, and Western Meadowlarks display intermediate habitat preferences with regional variation in their responses to disturbances (e.g., associated with recent disturbance in tallgrass prairie, associated with rested pastures in shortgrass prairie; Renfrew and Ribic 2001, Fritcher et al. 2004). The Upland Sandpiper was the only species that had an interaction between grazing and PDSI; however, the species had minimal variation in densities on grazed plots compared to ungrazed plots. Standing water on the ungrazed plots may have reduced suitability of ungrazed plots during extremely wet years for Upland Sandpipers or resulted in their movements to upland grasslands

Dickcissel and Red-winged Blackbird also displayed negative relationships with PDSI. Vegetation associations for Red-winged Blackbird appear more important than environmental conditions during selection of breeding habitat (Fletcher and Koford 2004). The association with PDSI may result from potential fluctuations in habitat suitability or in nest-site or prey availability while Dickcissels may respond to environmental conditions at either patch or regional scales. Drought conditions have been implicated as a proximate cause of Dickcissel irruptions in some areas (Taber 1947, Igl 1991). In addition, Dickcissel densities during dry or average PDSI years may be affected by interspecific interactions with Red-winged Blackbirds. To our knowledge, no studies have reported direct behavioral dominance of Red-winged Blackbirds over Dickcissels (Yasukawa and Searcy 1995, Temple 2002), although both species share similar nest-site selection (i.e., above ground nesters in grasslands). Dickcissels in the Platte River Valley initiate nesting 2–3 weeks after Red-winged Blackbirds, and the larger blackbird males often chase Dickcissel males from their territories (D. H. Kim, unpubl. data).

Cowbird densities in our study were higher in ungrazed plots compared to grazed plots, which is counter to information in the literature (e.g., Kostecke et al. 2003). Possible explanations include (1) regional cowbird densities are near capacity (Jensen and Cully 2005), (2) the spatial proximity of grazed pastures to ungrazed plots (<2 km) exert no energetic costs on female cowbirds moving among breeding and feeding areas (Goguen and Mathews 2001), or (3) host species' densities declined with grazing, offsetting the increased foraging opportunities for cowbirds. In our system, cowbird densities tracked Dickcissel and Red-winged Blackbird densities, but especially Bobolink densities, suggesting cowbirds may exploit the most common host species in the study area or that these four species share similar habitat preferences in this region

Available moisture may have profound effects on the avian community in sedge meadows and mesic grasslands. Declining species richness associated with drier conditions was consistent with other grassland bird studies (George et al. 1992, Zimmerman 1992), but declining densities with higher PDSI values suggests that sedge meadows and mesic grasslands may be less suitable for grassland birds during wet conditions. The pattern of increas-

ing density associated with drought conditions in the Platte River Valley appears opposite of other reported studies (e.g., Igl and Johnson 1999). Individual species have different habitat requirements; therefore, changes in vegetation structure and amount of standing water should affect species individually. For example, Igl and Johnson (1999) found abundance of Le Conte's Sparrow (*Ammodramus leconteii*) increased with moisture availability in grasslands enrolled in the Conservation Reserve Program in the northern Great Plains. This unexpected pattern from our study could result from riparian wet-meadow grasslands acting as a refugia for species escaping drier conditions in regional upland areas. Dry conditions may cause birds to move from upland sites as vegetation structure and habitat suitability deteriorates with drought conditions. During dry years, wet-meadow habitats should remain suitable longer during the breeding season given the higher water table and greater soil moisture compared to upland sites.

Van Horne (1983) cautioned against using density as an indicator of habitat quality, especially in disturbed habitats. Additional research focusing on reproductive success over several years will be required to measure the importance of both climate and grazing on reproductive success for all seven species. For example, in Oregon, drought lowered annual reproductive success for Bobolinks (Wittenberger 1982). Dry conditions also may limit food availability for adults and young. Although some insects, such as orthopterans, may increase during dry conditions, the availability and biomass of lepidopteran larvae may decrease, restricting growth rates for young nestlings unable to efficiently process chitonous prey. In either case, birds may be able to assess the potential of food or nest-site availability based on the condition of grasslands at the beginning of the breeding season (early May in Nebraska) and to adjust their breeding densities accordingly.

ACKNOWLEDGMENTS

We thank all of the people who helped collect the breeding bird data, especially T. E. Labedz, L. D. Igl, N. D. Niemuth, T. L. Shaffer, and 2 anonymous reviewers provided insightful comments that improved earlier versions of this manuscript. Work could not have been completed without the support of the U.S. Geological Survey's Northern Prairie Wildlife Research Center and Platte River Whooping Crane Trust. This is Platte River Whooping Crane Maintenance Trust manuscript # 0702.

LITERATURE CITED

Askins, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. Current Ornithology 11:1–34.

Bollinger, E. K. 1995. Successional changes and habitat selection in hayfield bird communities. Auk 112:720–730.

Bollinger, E. K. and T. A. Gavin. 1989. The effects of site quality on the breeding-site fidelity in Bobolinks. Auk 106:584–594.

Bragg, T. B. and A. A. Steuter. 1996. Prairie ecology—the mixed prairie. Pages 53–65 *in* Prairie conservation: preserving North America's most endangered ecosystem (F. B. Samson and F. L. Knopf, Editors). Island Press, Washington, D.C., USA.

Cody, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. BioScience 31:107–113.

Cody, M. L. 1985. Habitat selection in grassland and open-country birds. Pages 191–226 *in* Habitat selection in birds (M. L. Cody, Editor). Academic Press, Orlando, Florida, USA.

Currier, P., G. Lingle, and J. VanDerwalker. 1985. Migratory bird habitat on the Platte and North Platte rivers in Nebraska. Platte River Whooping Crane Trust, Grand Island, Nebraska, USA.

Dechant, J. A., M. F. Dinkins, D. H. Johnson, L. D. Igl, C. M. Goldade, B. D. Parkin, and B. R. Euliss. 1999. Effects of management practices on grassland birds: Upland Sandpiper. Version 12 August 2004. USDI, Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. www.npwrc.usgs.gov/resource/literatr/grasbird/upsa/upsa.htm (accessed 25 September 2007).

Dechant, J. A., M. L. Sondreal, D. H. Johnson, L. D. Igl, C. M. Goldade, M. P. Nenneman, and B. R. Euliss. 2003a. Effects of management practices on grassland birds: Grasshopper Sparrow. Version 12 August 2004. USDI, Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. www.npwrc.usgs.gov/resource/literatr/ grasbird/grsp/grsp.htm (accessed 25 September 2007).

Dechant, J. A., M. L. Sondreal, D. H. Johnson, L. D. Igl, C. M. Goldade, A. L. Zimmerman, and B. R. Euliss. 2003b. Effects of management practices on grassland birds: Bobolink. Version 12 August 2004. USDI, Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. www.npwrc.usgs.gov/resource/literatr/grasbird/bobo/ bobo.htm (accessed 25 September 2007).

Dechant, J. A., M. L. Sondreal, D. H. Johnson, L. D. Igl, C. M. Goldade, A. L. Zimmerman, and B. R. Euliss. 2003c. Effects of management practices on

grassland birds: Dickcissel. Version 12 August 2004. USDI, Geological Survey, Northern Prairie Wildlife Research Center. Jamestown, North Dakota, USA. www.npwrc.usgs.gov/resource/literatr/grasbird/ dick/dick.htm (accessed 25 September 2007).

Dechant, J. A., M. L. Sondreal, D. H. Johnson, L. D. Igl, C. M. Goldade, A. L. Zimmerman, and B. R. Euliss. 2003d. Effects of management practices on grassland birds: Western Meadowlark. Version 12 August 2004. USDI, Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. www.npwrc.usgs.gov/resource/literatr/grasbird/weme/weme.htm (accessed 27 September 2007).

Fletcher, R. J. and R. R. Koford. 2004. Consequences of rainfall variation for breeding wetland blackbirds. Canadian Journal of Zoology 82:1316–1325.

Fletcher, R. J., R. R. Koford, and D. A. Seaman. 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. Journal of Wildlife Management 70:145–157.

Fritcher, S. C., M. A. Rumble, and L. D. Flake. 2004. Grassland bird densities in seral stages of mixed-grass prairie. Journal of Range Management 57:351–357.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275–284.

Goguen, C. B. and N. E. Mathews. 2001. Brown-headed Cowbird behavior and movements in relation to livestock grazing. Ecological Applications 11:1533–1544.

Hay, M. A. and G. R. Lingle. 1982. 1981 Breeding bird censuses along the Platte River in south-central Nebraska. American Birds 36:105–106.

Henszey, R. J., K. Pfeiffer, and J. R. Keough. 2004. Linking surface- and ground-water levels to riparian grassland species along the Platte River in central Nebraska, USA. Wetlands 24:665–687.

Herkert, J. R. 1995. Analysis of Midwestern breeding bird population trends—1966–1993. American Midland Naturalist 134:41–50.

Herkert, J. R. 2003. Effects of management practices on grassland birds: Henslow's Sparrow. Version 12 August 2004. USDI, Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. http://www.npwrc.usgs.gov/resource/literatr/grasbird/hesp/hesp.htm (accessed 24 September 2007).

Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, D. H. Wolfe, S. K. Sherrod, M. A. Jenkins, J. Faaborg, and S. K. Robinson. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conservation Biology 17: 587–594.

Igl, L. D. 1991. The role of climate and mowing on Dickcissel (*Spiza americana*) movements, distribution, and abundance. Thesis. Iowa State University, Ames, USA.

Igl, L. D. and D. H. Johnson. 1999. Le Conte's Sparrows breeding in Conservation Reserve Program fields: precipitation and patterns of population change. Studies in Avian Biology 19:178–196.

Jensen, W. E. and J. F. Cully. 2005. Geographic variation in Brown-headed Cowbird (*Molothrus ater*) parasitism on Dickcissels (*Spiza americana*) in Great Plains tallgrass prairie. Auk 122:648–660.

Knopf, F. 1994. Avian assemblages on altered grasslands. A century of avifaunal change in western North American. Studies in Avian Biology 15: 232–246.

Kostecke, R. M., J. A. Koloszar, and D. C. Dearborn. 2003. Effect of a reduction in cattle stocking rate on Brown-headed Cowbird activity. Wildlife Society Bulletin 31:1083–1091.

Lingle, G. 1981. Mormon Island Crane Meadows—Protecting habitat for cranes along the Platte River, Nebraska. Pages 17–21 *in* Proceedings 1981 Crane Workshop (J. C. Lewis, Editor). National Audubon Society, Tavernier, Florida, USA.

Lingle, G. 1995a. 1994 Breeding bird census—Subirrigated grassland and native hay. Journal of Field Ornithology 66(supplement):111–112.

Lingle, G. 1995b. 1994 Breeding bird census—Wetland sedge meadow I and II. Journal of Field Ornithology 66(supplement):100–101.

Lingle, G. 1996a. 1995 Breeding bird census—Subirrigated grassland and native hay. Journal of Field Ornithology 67(supplement):86–87.

Lingle, G. 1996b. 1995 Breeding bird census—Wetland sedge meadow I and II. Journal of Field Ornithology 67(supplement):76–77.

Lingle, G. and P. Bedell. 1989a. 1988 Breeding bird census—Subirrigated native hay and grassland. Journal of Field Ornithology 60(supplement):60–61.

Lingle, G. and P. Bedell. 1989b. 1988 Breeding bird census—Wetland sedge meadow I and II. Journal of Field Ornithology 60(supplement):65–66.

Lingle, G. and P. Bedell. 1990a. 1989 Breeding bird census—Subirrigated grassland and native hay. Journal of Field Ornithology 61(supplement):72–73.

Lingle, G. and P. Bedell. 1990b. 1989 Breeding bird census—Wetland sedge meadow I and II. Journal of Field Ornithology 61(supplement):78–79.

Lingle, G. R. and K. L. Haugh. 1984a. 1983 Breeding bird census—Subirrigated grassland and native hay. American Birds 38:120.

Lingle, G. R. and K. L. Haugh. 1984b. 1983 Breeding bird census—Wetland sedge meadow I and II. American Birds 38:124–125.

Lingle, G. and W. S. Whitney. 1983a. 1982 Breeding

bird census—Subirrigated grassland and native hay. American Birds 37:101.

Lingle, G. and W. S. Whitney. 1983b. 1982 Breeding bird census—Wetland sedge meadow I and II. American Birds 37:104.

Lingle, G. and W. S. Whitney. 1991a. 1990 Breeding bird census—Subirrigated grassland and native hay. Journal of Field Ornithology 62(supplement): 84–85.

Lingle, G. and W. S. Whitney. 1991b. 1990 Breeding bird census—Wetland sedge meadow I and II. Journal of Field Ornithology 62(supplement):77–78.

Lingle, G., S. Bergman, and J. Liske. 1994a. 1993 Breeding bird census—Subirrigated grassland and native hay. Journal of Field Ornithology 65(supplement):122–123.

Lingle, G., S. Bergman, and J. Liske. 1994b. 1993 Breeding bird census—Wetland sedge meadow I and II. Journal of Field Ornithology 65(supplement):107–108.

Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. Second Edition. SAS Institute Inc., Cary, North Carolina, USA.

Milliken, G. A. and D. E. Johnson. 1984. Analysis of messy data. Volume I. Designed experiments. Van Nostrand Reinhold Co., New York, USA.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science, Kyushu University Series E 7:65–80.

Palmer, W. C. 1965. Meteorological drought. Research Paper Number 45. U.S. Department of Commerce, Weather Bureau, Washington, D.C., USA.

Renfrew, R. B. and C. A. Ribic. 2001. Grassland birds associated with agricultural riparian practices in southwestern Wisconsin. Journal of Range Management 54:546–552.

SAS Institute Inc. 2004. SAS Online Doc® 9.1.2. SAS Institute Inc., Cary, North Carolina, USA.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, results and analysis 1966–2004, Version 2004.1. USDI, Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.usgs.gov/bbs/bbs.html. (accessed 25 September 2007).

Steel, R. G. D. and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. Second Edition. McGraw-Hill Book Co., New York, USA.

Steinauer, E. M. and S. C. Collins. 1996. Prairie ecology–the tallgrass prairie. Pages 39–52 *in* Prairie conservation: preserving North America's most endangered ecosystem. (F. B. Samson and F. L. Knopf, Editors). Island Press, Washington, D.C., USA.

Taber, R. D. 1947. The Dickcissel in Wisconsin. Passenger Pigeon 9:39–46.

Temple, S. A. 2002. Dickcissel (*Spiza americana*). The birds of North America. Number 703.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Van Velzen, W. 1972. Breeding-bird census instructions. American Birds 26:1007–1010.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8:1–93.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43: 237–270.

Winter, M., D. H. Johnson, and J. A. Shaffer. 2005. Variability in vegetation effects on density and nesting success of grassland birds. Journal of Wildlife Management 69:185–197.

Wittenberger, J. F. 1980. Vegetation structure, food-supply, and polygyny in Bobolinks (*Dolichonyx oryzivorus*). Ecology 61:140–150.

Wittenberger, J. F. 1982. Factors affecting how male and female Bobolinks apportion parental investments. Condor 84:22–39.

Yasukawa, K. and W. A. Searcy. 1995. Red-winged Blackbird (*Agelaius phoeniceus*). The birds of North America. Number 184.

Zimmerman, J. L. 1992. Density-independent factors affecting the avian diversity of the tallgrass prairie community. Wilson Bulletin 104:85–94.

The Wilson Journal of Ornithology 120(4):830–839, 2008

RESPONSE OF SONGBIRDS TO RIPARIAN WILLOW HABITAT STRUCTURE IN THE GREATER YELLOWSTONE ECOSYSTEM

BRIAN F. M. OLECHNOWSKI[1,2] AND DIANE M. DEBINSKI[1]

ABSTRACT.—We compared the structure of riparian willow (*Salix* spp.) habitat and songbird diversity across two regions of the Greater Yellowstone Ecosystem: Gallatin National Forest and Yellowstone National Park in the north and Grand Teton National Park in the south. The average height of willows was greater (151 vs. 65.9 cm) in the Teton region, and the average density of willows was greater (45.2 vs. 26.1%) in the Gallatin. The average height of willows was the most important variable explaining songbird species richness and abundance across these two regions. Songbird richness and abundance was greater (6.1 vs. 3.1 species; 11.7 vs. 5.6 individuals) in the Teton region. Larger patch size in the Tetons could be a factor contributing to the higher level of diversity but was not statistically significant. Individual species responses to habitat structure varied based on the nesting height preference of the species. Species that nest above the ground or in taller vegetation had abundance positively correlated with average willow height (Yellow Warbler [*Dendroica petechia*] $P < 0.001$; Fox Sparrow [*Passerella iliaca*] $P = 0.001$). Yellow Warbler, Willow Flycatcher (*Empidonax trailii*), Fox Sparrow, and Common Yellowthroat (*Geothylpis trichas*) all had higher abundances in the Teton sites. The difference in willow habitat structure across these regions is likely influenced by historic differences in elk (*Cervus elaphus*) browsing in the northern regions of the Greater Yellowstone Ecosystem. *Received 4 September 2007. Accepted 26 February 2008.*

Many studies have examined how avian diversity responds to structural characteristics of habitat (MacArthur and MacArthur 1961, Jackson 1992, Yamaura et al. 2006). Most of this work has focused on bird species inhabiting prairie and forested ecosystems in North America (Cody 1974, Zimmerman 1992, Powell 2006, Sallabanks et al. 2006). These studies confirmed the importance of preserving and restoring prairie and forested ecosystems, but few studies have considered how avian biological diversity may respond to habitat changes in other environments. Montane riparian willows (*Salix* spp.) support the greatest diversity of songbird species in the semiarid portions of the western United States (Knopf et al. 1988, Dobkin et al. 1998). Thus, they warrant examination with respect to how their structure affects songbird diversity and abundance patterns.

Riparian plant communities dominated by willows in the mountain regions of the western United States provide a number of important ecological functions including stabilizing stream banks, moderating water temperatures and the surrounding microclimate, providing riparian corridors for dispersal of plants and vertebrates, and supporting a rich array of species from insects to birds to large ungulates and predators (Wingington and Beschta 2000, NRC 2002, Ripple and Beschta 2004b). Some willow habitats have been in decline for a number of decades (Singer et al. 1998). Peinetti et al. (2002) documented a 20% decline in riparian shrub cover and a 55% decline in tall willow cover in two valleys of Rocky Mountain National Park, Colorado. Ammon and Stacey (1997) and Berger et al. (2001) identified a number of songbird species including Yellow Warblers (*Dendroica petechia*), Willow Flycatchers (*Empidonax trailii*), Fox Sparrows (*Passerella iliaca*), and Calliope Hummingbirds (*Stellula calliope*) that were less abundant in areas where vegetative structure of willows had been altered by browsing.

Elk (*Cervus elaphus*) are the major native browsers of willows in the mountain west in the United States, and a number of studies in the Greater Yellowstone Ecosystem (GYE) have demonstrated decreased willow growth, reproduction, and cover in areas where elk are abundant (Kay and Chadde 1992; Ripple and Beschta 2004a, b). Competition for food, especially in the winter, has caused ungulate populations to browse on willows, aspen (*Populus tremuloides*), and cottonwood (*Populus* spp.) stands in the ecosystem (Romme et al. 1995, Ripple et al. 2001, Smith 2001). Singer

[1] Department of Ecology, Evolution, and Organismal Biology, 253 Bessey Hall, Iowa State University, Ames, IA 50014, USA.

[2] Corresponding author; e-mail: bolech@gmail.com

et al. (1994) found that 47% of willow communities in the winter range of elk in northern Yellowstone National Park had been height suppressed. Kay and Chadde (1992) studied long-term exclosures and found that elk reduced potential willow seed production on the northern range of Yellowstone by 100%. They concluded that some willows have not been able to produce seeds for the last 50 years.

The objectives of our study were to: (1) compare willow habitat structure in the northern and southern portions of the Greater Yellowstone Ecosystem, (2) examine how songbird communities respond to structure of willow habitat in this montane riparian system, and (3) discuss conservation implications of the relationship between avian diversity and willow structure in the GYE. We expected willow habitat to be more structurally complex in the Teton Valley (southern GYE) compared to the Gallatin (northern GYE) because of high levels of elk herbivory in the Gallatin River Valley (Singer et al. 1998; Ripple and Beschta 2004a, b). We hypothesized that songbird diversity would be directly correlated with the variables used to describe the vegetative structure of the willow habitat (height and density) of the vegetation.

METHODS

Study Area.—Our research was conducted in two areas of the Greater Yellowstone Ecosystem: Gallatin National Forest and northwest Yellowstone National Park (northern region of the GYE, hereafter referred to as the "Gallatin region"), and in Grand Teton National Park (southern region of the GYE, hereafter referred to as the "Teton region"). Nonforest cover types within the ecosystem range from hydric willow and sedge (*Carex* spp.) meadows to alpine rock meadows. The two regions have distinct landscapes and differ in average patch size, but support similar riparian willow habitat, plant, and songbird species (Debinski et al. 2001). Hydric meadows in the Gallatin region occur near creeks and rivers flowing along narrow valleys. The largest valleys are 1–3.3 km wide and up to 12.5 km long (Saveraid et al. 2001). The Teton region consists of large areas of sagebrush (*Artemisia* spp.) and willow flats with forested regions generally occurring on buttes, foothills, and mountains (Saveraid et al. 2001). The Teton Valley lies east of Jackson Lake and is 5–19 km wide and 76 km long (Saveraid et al. 2001).

Sampling Sites.—Sampling sites were established using remotely-sensed classification of the montane meadow habitats in the Greater Yellowstone Ecosystem to identify a moisture gradient in montane meadows. A map was produced that displayed this moisture gradient across meadows within the ecosystem. Hydric meadows, composed of riparian vegetation including willows, were identified using this map in 1997. Sites were considered suitable for sampling if they were at least 100 $\times$ 100 m in size, at least 500 m or farther from other sites, and within 8 km of a road or trail (Debinski et al. 2000). Willows had to be present at five of the 15 points (stops) at each site where we measured habitat structure to be included in our analysis. Eleven willow sites in the Gallatin and 14 sites in the Tetons met our criterion for analysis. Sites in the Gallatin were in the northwest region of Yellowstone National Park and within 10 km of the Gallatin River in the southeast region of Gallatin National Forest. Sites in the Tetons were within 8 km (east) of Jackson Lake in Grand Teton National Park near Moran, Wyoming. A center point was established at each site and was marked with a 1.25-m fiberglass or wooden post driven into the ground. UTM coordinates were taken at each center-point using a Global Positioning System to allow relocation of the points.

Willow Habitat Structure.—We assessed the three-dimensional structure of the willow vegetation at 25 sampling sites in July 2000. Vegetation sampling was limited to 1 year because of the intense effort required to obtain these data (4 people for 4 hrs/site). We assumed there were no major changes in grazing or browsing pressure, or effects of fire across years. We sampled the avifauna at each site annually between 1997 and 2001, and did not observe any qualitative differences in willow structure across these years (DMD, pers. obs.). Three 100-m transects were established at each site labeled "west", "center", and "east" and were aligned north-south at a distance of 30 m from each other. The center transect was placed through the pre-established site center. Five points, 20 m apart, were established along each transect, for a to-

tal of 15 points at each site. Data collected at each point included: vegetation type (grass, forb, shrub), maximum height of each vegetation type, and percent cover within each 10-cm vertical increment of the pole by that vegetation (modified from Robel et al. 1970). The pole used for density measurements was vertically partitioned into 10-cm segments up to 125 cm. Each segment was considered a "zone" and the percent density was estimated as: 0 = 0; 1–20 = 1; 21–40 = 20; 41–60 = 40, etc. Measurements were taken 1 m from the pole at each of the stops at a site. Percent density for all the points at a site was obtained by averaging across zones and points to provide an overall density value of the willows for that site. High density values were indicative of habitat that was consistently dense, while lower obscurity values were indicative of habitat that consists of "spaces" in the willow structure. The presence of willows could be assessed from 5 to all 15 of the possible points at each study site. We also recorded the specific willow species found at each site. The three major species in the Greater Yellowstone region are *S. wolfii*, *S. boothii*, and *S. bebbiana*. *Salix boothii* was the tallest of these three species, reaching 7 m at maturity, *S. bebbiana* reaches 3–4 m at maturity, and *S. wolfii* ranges from 0.5 to 1.5 m at maturity (USDA 2007). Relative abundance of these three species did not differ across the Gallatin and Teton regions (DMD and BFO, unpubl. data). Our analysis focuses on bird responses to vegetation structure rather than willow species composition because birds primarily choose where to nest or forage based on the physical structure of the habitat (Yamaura et al. 2006).

Bird Surveys.—Songbird density and abundance data were collected using 50-m radius point count surveys. Surveys were conducted at all 25 of our willow sites in 1999 (n = 11 in the Gallatin region, n = 14 in the Teton region), and at 12 of the 25 sites across the Gallatin region (n = 5) and Teton region (n = 7) in 1997–1998 and 2000–2001. These surveys were performed one to three times per year during 1997–2001 and from 0530–1030 hrs for each study site from late-May/early-June to mid-July. We only consider the first round of these surveys (during late May/early Jun) at each of our sampled sites due to uneven sampling effort (we were not able to repeat surveys at all sites after mid-June; the highest sampling size for sites was attained using only the first round of surveys conducted in late May/early Jun). Each survey involved two people recording and observing for 15 min. All researchers were trained in identifying birds by sight and sound. Birds were not surveyed if it was snowing or raining, but surveys were conducted if there was light frost or snow on the ground because bird activity was not reduced under these conditions (DMD, pers. obs.). Each individual bird seen and/or heard within the 50-m radius during a survey was recorded, and its location and distance from the observer were mapped. Flyovers were not included in the analysis because we were interested in those individuals that gave evidence of using the habitat for foraging or reproduction. Behaviors including singing, chirping, carrying nesting material, and feeding fledglings were also recorded (Gill 1995).

Statistical Analyses.—We used one-way analysis of variance (ANOVA) to assess differences in the three-dimensional structure of willow habitat (patch size, heights and densities of willows) between sites in the Gallatin region versus those in the Teton region. Simple and multiple linear regressions were used to examine the relationships of the vegetation variables and songbird species richness and abundance. Patch size was also considered in these analyses, and we compared patch sizes for our study sites using FRAGSTATS spatial analysis program (McGarigal and Marks 1994). We analyzed the songbird data for 1999 when all 25 sites were surveyed and for 1997–2001 when 12 sites were surveyed for multiple years. We averaged species richness and abundance at each site across years to examine how overall levels of diversity correlated with habitat measurements. These averages were also used to compare songbird species richness and abundance between the Gallatin and Teton regions. The effects of site and year were considered as co-factors when comparing abundances of nine individual species that used willow habitat across both regions of the GYE. We calculated the average annual abundance by region for each species, correcting for the number of sites surveyed. We considered year as a co-factor in this analysis because individual species did not show time

TABLE 1. Willow vegetation measurements in the Gallatin region (northern GYE) and the Teton region (southern GYE). Measurements were taken during summer 2000.

Category	Gallatin region (n = 11) $\bar{x} \pm$ SE	Teton region (n = 14) $\bar{x} \pm$ SE	F	P
Willow height, cm	65.9 ± 13.0	151.6 ± 11.6	24.2	<0.0001
Willow density, %	45.2 ± 4.1	26.1 ± 3.8	11.5	0.003
Patch size, ha	1.8 ± 80.5	252.8 ± 95.2	4.0	0.07
Extent of willows at site, %	70.8 ± 6.7	61.8 ± 6.0	1.0	0.33

trends in abundance during the years we recorded our observations. Multiple comparisons of species abundances across these two regions were corrected using the Bonferroni method. We calculated the average Shannon-Weaver Diversity Index (Shannon and Weaver 1962) across the 12 sites that were sampled between 1997 and 2001 to compare overall levels of songbird diversity between the two regions of the GYE. Analyses were performed using the statistical software package S-Plus Version 7.0 (Insightful Corp 2005).

RESULTS

Willow Structure in the Gallatin and the Tetons.—The overall three-dimensional structure of willow habitat was strikingly different when comparing the northern and southern regions of the GYE (Table 1). Willows in the Gallatin region were shorter and more dense, whereas willows in the Teton region were taller and less dense. Average willow heights and densities were negatively correlated (F = 14.8, df = 23, r^2 = 0.40, P = 0.0009). Average patch size of willow sites surveyed was much greater in the Teton region, but patch sizes of sites surveyed in this region varied considerably, and this difference was not significant (F = 4.0, df = 1, P = 0.07). The extent of willows surveyed at each site, (measured as the number of points where willows were present divided by 15) did not differ between the Gallatin and the Tetons (n = 11 for the Gallatin and n = 14 for the Tetons).

Willow Structure and Songbird Species Diversity in Willow Habitat of the GYE.—Two separate analyses were conducted to examine songbird abundance and richness versus vegetative structure. The first used all 25 sites where willows were measured and in which one round of bird surveys was completed in 1999. Average willow height was positively correlated with both songbird abundance (F = 6.2, df = 19, P = 0.022) and richness (F = 12.4, df = 19, P = 0.002) across sites in the multiple linear regression model (Table 2A). Patch size differences did not have a significant influence on either abundance or richness at our sites (F = 0.8, df = 19, P = 0.41; F = 2.8, df = 19, P = 0.13, respectively). The second analysis used the 12 willow sites in the Gallatin and Tetons that were surveyed over multiple years (1997–2001), including the data collected in 1999. Species richness and abundance were averaged at each site across this time period. Average willow height was positively correlated with average species richness (F = 6.1, df = 6, P = 0.04), but not with average species abundance (F = 4.7, df = 6, P = 0.06) (Table 2B). Differences in patch size at our sites were not significant in explaining abundance or richness of bird species across multiple years of surveys (F = 2.1, df = 6, P = 0.19; F = 3.5, df = 6, P = 0.10,

TABLE 2. Multiple linear regression models showing (A) Response of songbird abundance and richness to willow structure in 1999 across all 25 willow sites in the Greater Yellowstone Ecosystem. (B) Response of average songbird abundance and average songbird richness across 12 sites in which birds were surveyed from 1997 to 2001.

	Songbird abundance		Songbird richness	
Category	F	P	F	P
(A)				
Willow height	6.2	0.022	12.4	0.002
Willow density	0.4	0.52	1.3	0.67
Height × density	0.5	0.48	0.05	0.82
Patch size	0.8	0.41	2.8	0.13
(B)				
Willow height	4.7	0.06	6.1	0.040
Willow density	0.7	0.44	0.1	0.73
Height × density	1.7	0.22	2.3	0.17
Patch size	2.1	0.19	3.5	0.10

TABLE 3. (A) Average songbird species richness and abundance across 25 willow sites in the Greater Yellowstone Ecosystem in 1999. (B) Average songbird species richness, abundance, and the Shannon-Weaver Index across 12 sites in which birds were surveyed from 1997 to 2001.

	Gallatin region $\bar{x} \pm$ SE	Teton region $\bar{x} \pm$ SE	*F*	*P*
(A)	(n = 11)	(n = 14)		
Abundance	5.4 ± 1.1	8.8 ± 0.9	4.7	0.040
Richness	3.2 ± 0.8	5.8 ± 0.6	5.3	0.030
(B)	(n = 5)	(n = 7)		
Abundance	5.6 ± 2.0	11.7 ± 1.4	38.0	0.0001
Richness	3.1 ± 1.3	6.1 ± 1.1	19.3	0.001
Shannon-Weaver Index	0.9 ± 0.4	1.66 ± 0.2	15.7	0.003

respectively). None of the habitat variables (willow height, willow density, patch size, extent of willows) was significantly related to average species abundance across multiple years, but average willow height was the most important variable in this model when explaining both songbird species richness and abundance.

Songbird Diversity in the Tetons and Gallatin.—Two separate analyses were conducted to examine differences in overall songbird richness and abundance in the Teton and Gallatin regions. The first used all 25 sites where willows were measured and for which one round of bird surveys was completed in 1999. The Tetons had higher levels of both songbird species richness (F = 5.3, df = 1, P = 0.030) and abundance (F = 4.7, df = 1, P = 0.040) (Table 3A). The second analysis used the 12 willow sites in the Gallatin and Tetons that were surveyed across multiple years (1997–2001). The Tetons had higher levels of both average songbird species richness (F = 19.3, df = 1, P = 0.001) and average abundance (F = 38.0, df = 1, P = 0.0001). The average Shannon-Weaver Index of Diversity was also greater in the Teton region (F = 15.7, df = 1, P = 0.003) (Table 3B).

Individual Species Responses.—Four of nine individual species across the Gallatin and Teton regions (data pooled from the sites within each region and across years in which surveys were conducted) were more abundant in the Teton region (Table 4). These four species were Yellow Warbler (F = 46.2, df = 1, P < 0.0001), Fox Sparrow (F = 12.0, df = 1, P = 0.008), Common Yellowthroat (*Geothlypis trichas*) (F = 9.6, df = 1, P = 0.030), and Willow Flycatcher (F = 7.5, df = 1, P = 0.040). Abundance of three of these four species was significantly correlated with average willow height at 12 sites across both regions of the GYE: Yellow Warblers (P < 0.001, r^2 = 0.26), Fox Sparrows (P = 0.001, r^2 = 0.16), and Willow Flycatchers (P = 0.045, r^2 = 0.07) (Fig. 1.). The average abundance of three other species did not differ across the two regions of the GYE, but still had a posi-

TABLE 4. Average annual abundance by region for nine species of songbirds that used willow habitats in the Greater Yellowstone Ecosystem from 1997 to 2001, corrected for number of sites surveyed in each region.

	Gallatin region (n = 5) $\bar{x} \pm$ SE	Teton region (n = 7) $\bar{x} \pm$ SE	*F*	*P*
Yellow Warbler	0.2 ± 0.1	2.5 ± 0.3	46.2	<0.0001
Lincoln's Sparrow	2.0 ± 0.4	1.7 ± 0.2	0.4	1.0
Willow Flycatcher	0.1 ± 0.1	0.5 ± 0.1	7.5	0.040
Fox Sparrow	0 ± 0	0.5 ± 0.1	12.0	0.008
Common Yellowthroat	0.4 ± 0.1	1.5 ± 0.3	9.6	0.030
Dusky Flycatcher	0.1 ± 0.4	0.3 ± 0.6	1.0	1.0
American Robin	0.2 ± 0.1	0.3 ± 0.1	0.5	1.0
Song Sparrow	0.3 ± 0.2	0.5 ± 0.2	0.6	1.0
White-Crowned Sparrow	0.1 ± 0.1	0.5 ± 0.2	3.0	0.81

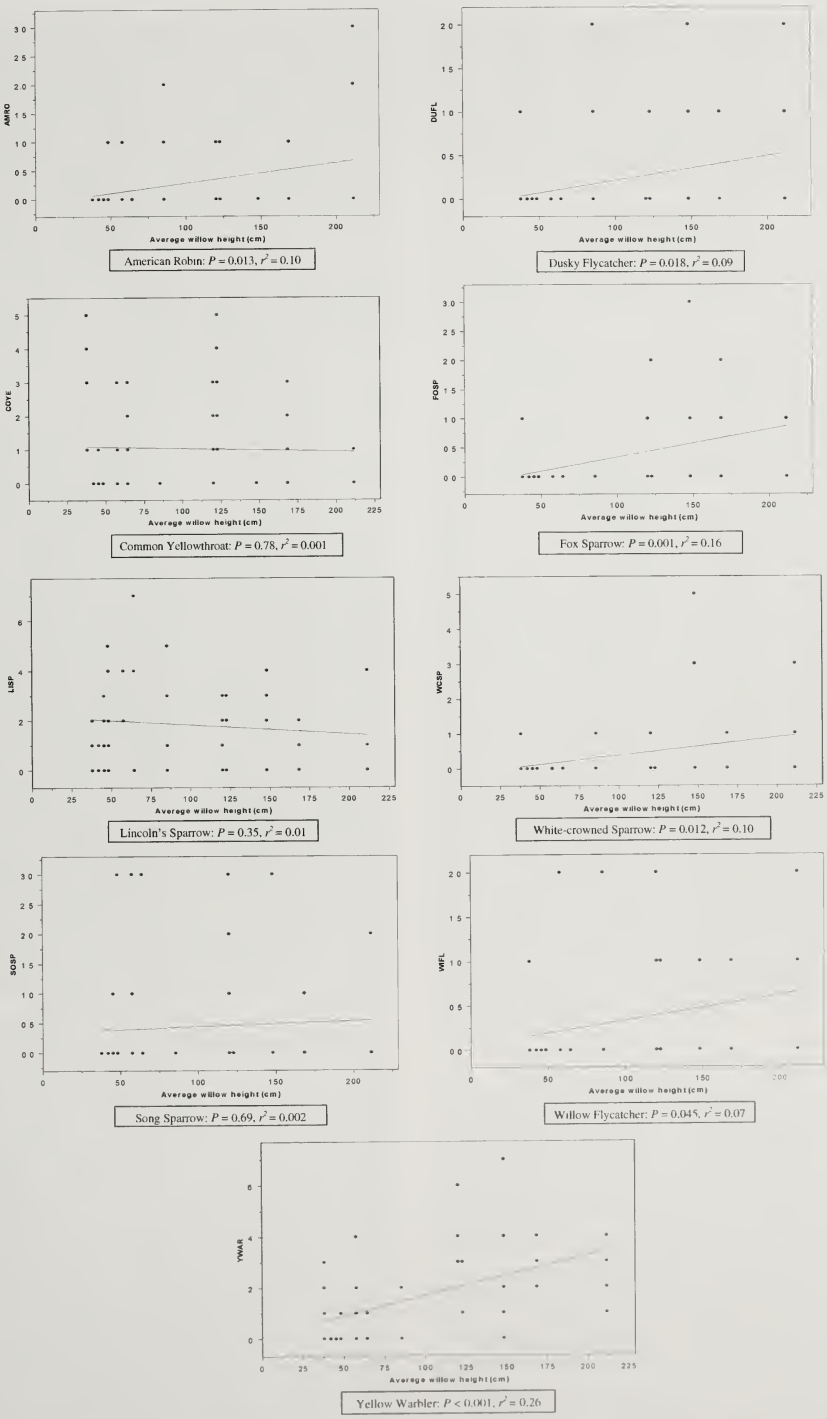


FIG. 1. Relationship of individual species abundances with average willow heights (cm) at 12 sites in the Greater Yellowstone Ecosystem. Songbird abundance data are pooled across 1997 to 2001.

tive correlation with willow height. These species include Dusky Flycatcher (*Empidonax oberholseri*) ($P = 0.018$, $r^2 = 0.09$), American Robin (*Turdus migratorius*) ($P = 0.013$, $r^2 = 0.10$), and White-crowned Sparrow (*Zonotrichia leucophrys*) ($P = 0.012$, $r^2 = 0.10$).

DISCUSSION

Differences in Willow Habitat Structure and Songbird Diversity.—Willow habitat was more structurally complex in the Teton than the Gallatin region and this habitat complexity was reflected in abundance and distribution of willow-dependent songbirds. Willows in the Teton region were taller and were less dense. Levels of overall songbird diversity and abundance were positively correlated with height of willows, and a greater number of individual songbirds and species were recorded in the Teton region. We acknowledge that larger patch size of willows in the Tetons could be a contributing variable for greater songbird species richness and abundance in the Teton region (despite the lack of statistical significance). However, other studies have also reported vegetation height as an important variable in explaining songbird species richness and abundance in forested (Barbaro et al. 2005) and prairie systems (Zalba and Cozzani 2004). The abundance of several individual species had a significant positive relationship with average willow height across the Gallatin and Teton regions. Yellow Warblers and Fox Sparrows had the strongest positive relationship with average willow height. Our results build on those of Berger et al. (2001) who conducted a similar study in the GYE and reported that structure of willow vegetation influences songbird species richness and abundance. Our study strengthens the biological signal of these patterns because we conducted bird surveys over multiple years (vs. 1 yr, Berger et al. 2001) and we surveyed a larger number of sites than Berger et al. (2001 [$n = 6$]).

High levels of herbivory can have cascading effects on species diversity and abundance across a variety of taxa, including plants, birds, and herbivores (McLaren and Peterson 1994: Ripple et al. 2001; Ripple and Beschta 2004a, b; Beyer 2007). Elk numbers and herbivory increased during the period of time gray wolves (*Canis lupus*) were absent and elk control efforts (shooting and trapping) were relatively low in the GYE (mid 1920s to 1995) and, as a result of overbrowsing, willow recruitment decreased (Kay 1990; Kay and Chadde 1992; Singer et al. 1994, 1998; Ripple and Larsen 2000; Ripple et al. 2001; Ripple and Beschta 2004a, b; Beyer 2007). Our research demonstrates that willow habitats characterized by shorter willow vegetation have lower levels of songbird species richness and abundance. Songbirds use these habitats for foraging and nesting, and these activities may be affected by herbivory. Historically, winter populations of elk have been lower in the Teton region because many elk in the southern region of the GYE spend their winters on the National Elk Refuge (NER) in Jackson Hole, where supplemental food sources are provided (Smith et al. 2004). The additional food provided at the refuge has likely decreased browsing on willows within boundaries of Grand Teton National Park. Anderson (2007) reported that feed stations at the NER attract elk that browse on willows in the surrounding area, and effectively decrease willow height, songbird species richness, and songbird abundance. Our study sites were not near these feeding stations, but the Anderson (2007) study emphasizes that intense elk browsing negatively affects willow habitat and songbird communities. These historical patterns in elk abundance and grazing across the GYE are likely contributing factors in explaining the striking structural difference in willow habitat across our two regions of study.

Ungulate browsing in the northern GYE has also affected American beaver (*Castor canadensis*) populations, which may be affecting riparian willow habitats. No beaver were documented on the northern range of the ecosystem during 1996, shortly after gray wolf reintroduction (Smith et al. 2003). Collins (1976) and Gribb (2004) documented active beaver dens in the Teton region during their studies. Ripple and Beschta (2004a) suggested that as elk increased in abundance in the northern range of the GYE through the mid to late 1900s, beaver populations declined and became practically extinct. Beaver occurred in the northern GYE before wolves were extirpated in 1926 (Warren 1926, Jonas 1955). The overall vigor and success of willows is related to activity of beaver populations because beaver affect the level of surface water in the ri-

parian environment (Ripple and Beschta 2004b). Medin and Clary (1990) also reported that avian species richness in riparian habitat of the mountain west was greater in ponds with beaver activity. Naiman et al. (1988) and Pollock et al. (1995) indicated that beaver can increase plant, invertebrate, and vertebrate diversity in the system.

Individual Species Responses.—We found varying abundances of nine songbird species that use riparian willow habitats, but those species that nest higher in the willow vegetation showed consistent trends. Yellow Warblers, Fox Sparrows, Willow Flycatchers, and Common Yellowthroats were significantly more abundant in the Tetons (where willow heights were greater), and other species (e.g., Lincoln's Sparrow [*Melospiza lincolnii*], American Robin, White-crowned Sparrow) had no clear difference in abundance levels. Berger et al. (2001) found that Yellow Warblers, Fox Sparrows, and Willow Flycatchers declined in areas that were heavily grazed by moose (*Alces alces*). White-crowned Sparrow and Lincoln's Sparrow were found in greater abundances in more heavily grazed areas in Berger's (2001) study. Additionally, Anderson (2007) found that Fox Sparrows and Willow Flycatchers were especially sensitive to habitat changes due to elk browsing. Reasons for differential responses among songbirds may be explained by nest placement. Salt (1957) indicated Lincoln's Sparrow and White-crowned Sparrow nest closer to the ground level in the GYE (and generally reside in lower vegetation) where herbivory impacts would presumably not be as great. Data from Ammon and Stacey (1997) and Berger et al. (2001) suggests that ground nesting birds are less affected by grazing than species that nest above ground. In contrast, Yellow Warblers, Willow Flycatchers, and Fox Sparrows prefer to reside and nest in taller vegetation. Yellow Warblers, in particular, nest much higher above ground level. Thus, it is not surprising that Yellow Warblers had the most pronounced difference in abundance across the Gallatin and Teton regions, and had the strongest positive relationship with willow height. If tall willows are not available, songbird species that nest high in willows may be absent from these ecological communities. Species that are more generalist in habitat selection and tend to nest lower in willows (e.g., American Robin, White-crowned Sparrow, Song Sparrow [*Melospiza melodia*]) had fewer differences in abundance levels across the Gallatin and Teton regions. These species choose between a number of different habitats to forage and nest, and their patterns of presence in riparian willow habitat may be more haphazard than a willow specialist, such as Willow Flycatcher.

CONSERVATION IMPLICATIONS

Willows in the Teton region were taller and less dense than those in the Gallatin region. This difference in willow height and density had strong correlations with differences in songbird abundance and diversity patterns. The most reasonable mechanism causing this difference has been high levels of herbivory by elk in the northern part of the system, especially during winter when food is scarce. A number of other studies have examined how populations of ungulates can cause woody vegetation in the Rocky Mountain region of the United States to decline (White et al. 1998, Ripple and Larsen 2000, Beschta 2003). Riparian songbird communities are influenced by the structural characteristics of the habitat, and this structure could differentially affect avian species based on their specific life history characteristics. Our findings suggest that songbirds that nest in the uppermost portions of tall willows may be particularly affected by elk herbivory.

ACKNOWLEDGMENTS

We thank the University of Wyoming, National Park Service Research Center (AMK Ranch; H. F. Harlow, Director) for funding and accommodating our research team. Data collection was funded by a grant from the Environmental Protection Agency (EPA) through their Ecological Assessment and Restoration program. Products of this grant, although funded by the EPA (through grant 96-NCERQA-1A Debinski et al.) have not been subjected to the Agency's peer review and do not necessarily reflect the views of the Agency and no official endorsement should be inferred. Statistical consulting was provided by D. H. Cook. Graphics assistance was provided by J. W. Morphew. We thank the many field technicians who helped over the years.

LITERATURE CITED

Ammon, A. M. and P. B. Stacey. 1997. Avian nest success in relation to past grazing regimes in a montane riparian system. Condor 99:7–13.

Anderson, E. M. 2007. Changes in bird communities and willow habitats associated with fed elk. Wilson Journal of Ornithology 119:400–409.

Barbaro, L., L. Pontcharraud, F. Vetillard, D. Guyon, and H. Jactel. 2005. Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. Ecoscience 12:110–121.

Berger, J., P. B. Stacey, L. B. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11: 947–960.

Beschta, R. L. 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. Ecological Applications 13:1295–1309.

Beyer, H. L. 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? Ecological Applications 17:1563–1571.

Cody, M. L. 1974. Competition and structure of bird communities. Princeton University Press, Princeton, New Jersey, USA.

Collins, T. C. 1976. Population characteristics and habitat relationships of beavers, *Castor canadensis*, in northwest Wyoming. Dissertation. University of Wyoming, Laramie, USA.

Debinski, D. M., M. E. Jakubauskas, and K. Kindscher. 2000. Montane meadows as indicators of environmental change. Environmental Monitoring and Assessment 64:213–225.

Debinski, D. M., C. Ray, and E. H. Saveraid. 2001. Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity? Biological Conservation 98:179–190.

Dobkin, D. S., A. C. Rich, and W. H. Pyle. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. Conservation Biology 12: 209–221.

Gill, F. B. 1995. Ornithology. Second Edition. W. H. Freeman and Company, New York, USA.

Gribb, W. J. 2004. Development of a potential beaver habitat model for the Snake River Basin, Grand Teton National Park, Wyoming. Pages 31–40 *in* 28th Annual Report, UW-NPS Research Station, Jackson Lake, Wyoming, USA.

Insightful Corp. 2005. S-Plus Version 7.0. Seattle, Washington, USA.

Jackson, S. G. 1992. Relationships among birds, willows, and native ungulates in and around northern Yellowstone National Park. Thesis. Utah State University, Logan, USA.

Jonas, R. J. 1955. A population and ecological study of the beaver (*Castor canadensis*) in Yellowstone National Park. Thesis. University of Idaho, Moscow, USA.

Kay, C. E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. Dissertation. Utah State University, Logan, USA.

Kay, C. E. and S. Chadde. 1992. Reduction of willow seed production by ungulate browsing in Yellowstone National Park. Pages 92–99 *in* Proceedings: symposium on ecology and management of riparian shrub communities, 29–31 May, 1991 (W. P. Clary, E. D. McArthur, D. Bedunah, and C. L. Wambolt, Editors). General Technical Report INT-289. USDA, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Knopf, F. L., J. A. Sedgwick, and R. W. Cannon. 1988. Guild structure of riparian avifauna relative to seasonal cattle grazing. Journal of Wildlife Management 52:280–290.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

McGarigal, K. and B. J. Marks. 1994. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Version 2.0. Oregon State University, Corvallis, USA.

McLaren, B. E. and R. O. Petersen. 1994. Wolves, moose and tree rings on Isle Royale. Science 266: 1555–1558.

Medin, D. E. and W. P. Clary. 1990. Bird populations in and adjacent to a beaver pond ecosystem in Idaho. Research Paper INT-432. USDA, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver (*Castor canadensis*). BioScience 38:753–762.

National Research Council (NRC). 2002. Ecological dynamics on Yellowstone's northern range. National Academy Press, Washington D.C., USA.

Peinetti, H. R., M. A. Kalkhan, and M. B. Coughenour. 2002. Long-term changes in willow spatial distribution on the elk range of Rocky Mountain National Park, USA. Landscape Ecology 17:341–354.

Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Paster, and G. Pinay. 1995. Beaver as engineers: influences of biotic and abiotic characteristics of drainage basins. Pages 117–126 *in* Linking species and ecosystems (C. G. Jones and J. H. Lawton, Editors). Chapman and Hall, New York, USA.

Powell, A. F. L. A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. Auk 123:183–197.

Ripple, W. J. and R. L. Beschta. 2004a. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755–766.

Ripple, W. J. and R. L. Beschta. 2004b. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of southwestern Montana. Forest Ecology and Management 200:161–181.

Ripple, W. J. and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park. Forest Ecology and Management 184:299–313.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk, and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227–234.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23: 295–297.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76:2097–2106.

Sallabanks, R., R. A. Riggs, L. E. Cobb, and S. W. Dodson. 2006. Bird-habitat relationships in grand fir forests of the Blue Mountains, Oregon. Forest Science 52:489–502.

Salt, G. W. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59:373–393.

Saveraid, E. H., D. M. Debinski, K. Kindscher, and M. E. Jakubauskas. 2001. A comparison of satellite data and landscape variables in predicting bird species occurrences in the Greater Yellowstone Ecosystem, USA. Landscape Ecology 16: 71–83.

Shannon, C. E. and W. Weaver. 1962. The mathematical theory of communication. University of Illinois Press, Urbana, USA.

Singer, F. J., L. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26:419–428.

Smith, B. 2001. Winter feeding of elk in western North America. Journal of Wildlife Management 65: 173–190.

Smith, B., E. K. Cole, and D. S. Dobkin. 2004. Imperfect pasture: a century of change at the National Elk Refuge in Jackson Hole Wyoming. Grand Teton National History Association, Moose, Wyoming, USA.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. BioScience 53: 330–340.

U.S. Department of Agriculture (USDA). 2007. USDA plants database. http://plants.usda.gov/ (accessed 16 January 2007).

Warren, E. R. 1926. A study of beaver in the Yancey region of Yellowstone National Park. Roosevelt Wild Life Annals 1:1–191.

White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildlife Society Bulletin 26:449–462.

Wingington Jr., P. J. and R. L. Beschta. 2000. Riparian ecology and management in multi-land use watersheds. American Water Resources Association, Middleburg, Virginia, USA.

Yamaura, Y., K. Katoh, and T. Takahashi. 2006. Reversing habitat loss: deciduous habitat fragmentation matters to birds in a larch plantation matrix. Ecography 29:827–834.

Zalba, S. M. and N. C. Cozzani. 2004. The impact of feral horses on grassland bird communities in Argentina. Animal Conservation 7:35–44.

Zimmerman, J. L. 1992. Density-independent factors affecting the avian diversity of the tallgrass prairie community. Wilson Bulletin 104:85–94.

The Wilson Journal of Ornithology 120(4):840–855, 2008

REGIONAL ANALYSIS OF RIPARIAN BIRD SPECIES RESPONSE TO VEGETATION AND LOCAL HABITAT FEATURES

NADAV NUR,[1,2] GRANT BALLARD,[1] AND GEOFFREY R. GEUPEL[1]

ABSTRACT.—We investigated relationships between riparian bird abundance and local vegetation characteristics and habitat features across the Sacramento/San Joaquin Valley, California. Number of detections was analyzed for each of 21 species from point count surveys over a 4-year period at 22 sites from three regions (Sacramento River, Cosumnes River, and San Joaquin River) in relation to 16 measures of habitat and vegetation composition within 50 m of 184 survey points. Tree variables, including tree height and trunk diameter, were often important, as was specific composition of tree species, especially Fremont cottonwood (*Populus fremontii*) and valley oak (*Quercus lobata*). Effects of mugwort (*Artemisia douglasiana*) and blackberry (*Rubus* spp.) were generally positive. The median partial R^2 due to vegetation/habitat characteristics was 16% after controlling for regional differences in abundance per species. Comparisons of model results at the local versus regional scale revealed spatial variation in bird abundance was independent of spatial variation in habitat variables. The effect of a habitat variable differed among the three regions for 11 of 16 variables. Models that used one or more of the first three principal components (extracted from the 16 vegetation and habitat variables) had substantially lower predictive ability than models built using individual variables. The results emphasize the importance of both understory vegetation and tree characteristics at different spatial scales. Local vegetation and habitat characteristics are important in explaining variation in local abundance, but there is a need to develop models specific to each subregion. *Received 28 July 2006. Accepted 1 March 2008.*

Riparian habitat in the western United States is one of the most productive and valuable habitats for all wildlife, especially in California (Knopf 1985, Rich 2002, Faber 2003). It is also one of the most threatened habitats, with only 5% of California's original riparian habitat remaining (Katibah 1984, Abell 1989). Riparian restoration and management of riparian habitat have become management priorities for agencies and non-governmental organizations throughout California (RHJV 2004).

Successful management and conservation of birds using riparian habitat requires information on how birds respond to habitat characteristics, including changes resulting from habitat degradation or restoration. Specific information is needed regarding elements or attributes of habitats used by avian species. Earlier studies on bird-habitat associations emphasized general structural characteristics of vegetation (Lack 1933, Hildén 1965, Wiens 1969, Willson 1974, Cody 1985), but more recent studies have identified the importance of specific tree species for riparian-dependent birds (Strong and Bock 1990, Saab 1999). This is consistent with findings of Wiens and Rotenberry (1981) that shrub-steppe birds respond more strongly to specific shrub species than to general vegetation and habitat structure. Riparian vegetation is composed of ground cover, herbs and forbs, shrubs, and trees; few studies have examined the importance of all components (Heath and Ballard 2003).

We also do not know the spatial scale at which birds respond. Previous riparian studies have either had broad spatial coverage (e.g., Tewksbury et al. 2002) or have examined factors influencing abundance at the local, territory-level scale (e.g., Strong and Bock 1990), but have rarely combined both components. Saab (1999) concluded that regional-scale factors were more important than local habitat factors in explaining variation in riparian bird abundance, but this conclusion has not been supported in other studies (Scott et al. 2003).

Little information is available as to whether bird-habitat correlations at a site or cluster of sites apply across larger spatial scales (e.g., across different watersheds or regions). This limits our ability to successfully generalize management recommendations based on one local study to that of other populations.

Riparian bird studies have often examined community-wide metrics (i.e., species diversity or richness), but relatively few have analyzed species-specific patterns of abundance

[1] PRBO Conservation Science, 3820 Cypress Drive, #11, Petaluma, CA 94954, USA.

[2] Corresponding author; e-mail: nnur@prbo.org

for a wide variety of species. Bird species diversity is a useful metric (MacArthur and MacArthur 1961), but does not indicate how individual species respond to specific habitat features, which may vary by species (Howell et al. 2000). Studies focused on a few "focal" species can be informative, but raise the question of how representative findings or predictions are for the entire community (Chase et al. 2000).

We investigated relationships between the abundance of 21 landbird species (20 passerines and 1 near-passerine) and local habitat or vegetation characteristics at 22 sites spanning 400 km of the Central Valley of California, including the Sacramento, San Joaquin, and Cosumnes rivers. All sites were classified as "valley-foothills riparian habitat" (Mayer and Laudenslayer 1988). Specific objectives were to develop and evaluate statistical predictive models for each of the 21 species to: (1) identify which vegetation or habitat variables (hereafter habitat variables) explain variation in abundance in each species at the local scale, (2) characterize commonalities and differences among bird species in the variables of influence and direction of their influence, (3) examine the consistency of effects of these variables for each species across three different regions of the Central Valley, (4) quantify the magnitude of variation in abundance of individual species explained by variation in habitat characteristics at the local scale, and (5) compare predictive abilities of models based on principal components with models based on the individual habitat variables.

METHODS

Study Sites.—There were three study areas: along the Middle Sacramento River, Cosumnes River, and San Joaquin River, all within the Sacramento/San Joaquin River watershed (Fig. 1). Studies in the Sacramento River region were conducted at 10 sites, spanning 160 km between Colusa and Red Bluff (n = 84 point count stations). Data were collected at six sites in the Cosumnes River region spanning ~15 km (n = 44 point count stations). Data in the San Joaquin River region were collected at six sites within the San Luis National Wildlife Refuge spanning ~20 km (n = 54 point count stations).

Field Methods.—Point count surveys (Ralph et al. 1993, 1995) were conducted three times per breeding season during May and early June. Surveys were conducted in 4 years, 1995–1998 for Cosumnes and Sacramento river sites, and 1995–1997 for San Joaquin sites. All species detected within 50 m of the observer were recorded over a 5-min period at each point count station. Surveys were conducted beginning 15 min after sunrise and concluding within 4 hrs of sunrise. Surveys were not conducted during rainy or excessively windy conditions. Stations were 200–250 m apart and in all habitats within a site; only those in riparian habitat (vs. those in crops, grasslands, orchards, etc.) were included in this study.

Fine-scale vegetation and habitat assessment were conducted at all point count stations at least once during 1995–1997. We used the most recent year of data if vegetation was surveyed in more than 1 year; there was no assessment of change in vegetation during the survey period. We used a modified version of the relevé (Estimation of Stand Characteristics) method of vegetation assessment following Ralph et al. (1993). Vegetation at each point count station was assessed using a 50-m radius (0.785 ha) plot centered on the point count survey station. General characteristics of the plot were recorded (including maximum tree dbh, tree height, presence of water, etc.), and cover, abundance, and height of each vegetation stratum (tree, shrub, herb) were estimated. These were defined following Ralph et al. (1993) with respect to height from ground, not botanically. The tree layer was >5 m, the shrub layer was 0.5 to 5 m, and the herb layer was <50 cm. Species composition and species richness of trees and shrubs were ascertained within each vegetation stratum. Percent absolute cover was recorded for each species. All willows (*Salix* spp.) were pooled for analysis. A given species could be recorded either as shrubs or trees depending on height. Presence of water was defined with respect to open water within the 50-m radius (1 if water present within 50 m, 0 otherwise).

Selection of Habitat Variables.—We considered 16 habitat variables, with region as an additional analytical variable (Table 1). We chose variables that we considered potentially biologically relevant and/or of management interest (Heath and Ballard 2003). A principal

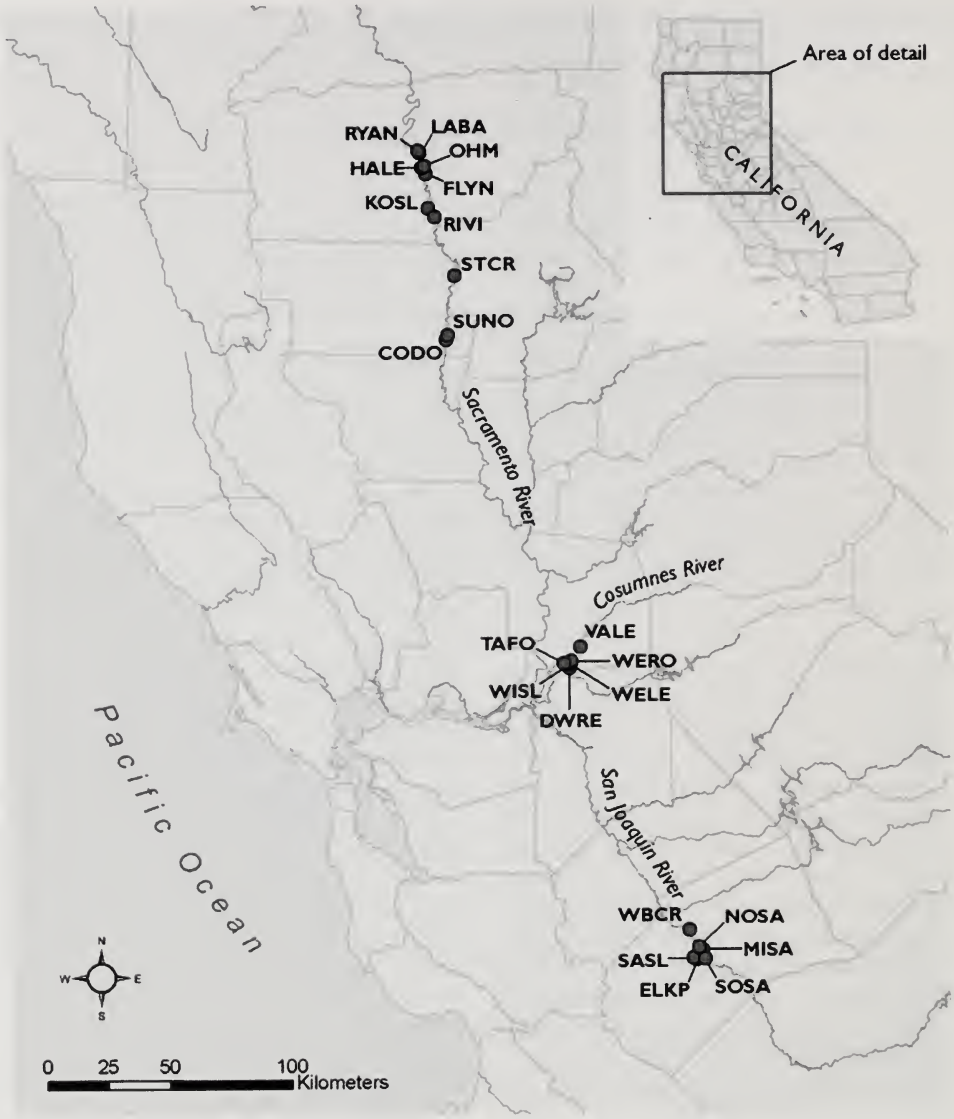


FIG. 1. Study area, showing 3 regions (Sacramento, Cosumnes, and San Joaquin rivers). Sites within region with four letter abbreviations, from north to south: RYAN = Ryan; LABA = Labaranca; OHM = Ohm; HALE = Haleakala; FLYN = Flynn; KOSL = Kopta Slough; RIVI = River Vista; STCR = Stony Creek; SUNO = Sul Norte; CODO = Codora; VALE = Valensin; TAFO = Tall Forest; WERO = Wendell's Road; WELE = Wendell's Levee; WISL = Wilson's Slough; DWRE = DWR East; WBCR = West Bear Creek; NOSA = North San Joaquin; MISA = Middle San Joaquin; SASL = Salt Slough; ELKP = Elk Pasture; and SOSA = South San Joaquin.

criterion for selection of vegetation variables was adequacy of representation in at least two of the three regions. Shrub, tree, or herb species prevalent in only one region were not included, nor were plant species that were uncommon. Preliminary analyses indicated that transformations of maximum tree height and dbh provided better predictors of bird abundance than untransformed values for each variable. We used tree height index (Table 1) and the natural log of maximum tree dbh for analyses. The transformation allowed for non-linear, monotonic effects of tree height or maximum tree dbh on abundance.

TABLE 1. Principal component analysis (n = 178) for 16 vegetation and habitat variables. Loadings for the first five principal components. Variables with loadings of absolute value ≥0.35 indicated by*.

Variable	Mean	Eigenvectors				
		I	II	III	IV	V
Water (Yes = 1; No = 0)	0.55	0.046	0.285	0.445*	−0.166	0.109
Tree cover (%)	35.1	0.318	−0.317	0.075	−0.217	−0.264
Shrub cover (%)	24.5	0.289	0.288	−0.127	0.395*	−0.108
Herb cover (%)	34.1	−0.383*	0.116	0.029	−0.162	0.290
Tree species richness	3.42	0.357*	0.177	−0.109	0.097	0.079
Shrub species richness	4.31	0.305	0.266	−0.172	0.044	0.168
Tree dbh index[a]	3.68	0.287	−0.124	0.353*	−0.081	0.242
Tree height index[b]	3.20	0.340	−0.269	−0.056	−0.029	0.243
Willow shrub cover (%)	7.88	−0.012	0.165	0.362*	0.478*	0.007
Willow tree cover (%)	12.7	−0.047	0.014	0.537*	−0.011	−0.354*
Cottonwood tree cover (%)	4.23	0.116	−0.470*	−0.193	−0.015	−0.178
Valley oak shrub cover (%)	0.84	−0.106	0.2556	−0.329	0.175	−0.381*
Valley oak tree cover (%)	6.13	0.225	0.264	−0.073	−0.401*	0.226
Blackberry cover (%)	3.12	0.269	0.302	−0.053	−0.221	−0.089
Mugwort cover (%)	2.40	0.008	−0.228	0.003	0.471*	0.498*
Grass cover (%)	15.0	−0.315	0.074	−0.192	−0.181	0.246

[a] Index = ln(maximum tree dbh + 1); maximum tree dbh measured in cm, 0 if no trees present.
[b] Scored 0 if no trees; otherwise 1, 2, 3, 4, or 5, classifying height into groups corresponding to: <9, 9 to <13, 13 to <18, 18 to <25, and ≥25 m.

Distinguishing the potential effect of California blackberry (*Rubus ursinus*) from Himalayan blackberry (*R. discolor*) on bird species was of management interest (native vs. non-native invasive), but California blackberry was either uncommon or absent from most sites. Thus, we analyzed only the summed blackberry cover.

Selection of Avian Species for Analysis.—We focused on landbird species known to breed in the study region (presence throughout the breeding season, mist net captures, and nest-monitoring at nearby sites). We selected the 20 most abundant species based on detections at point count stations in the riparian sites. Four of the 20 species were identified as focal species by the Riparian Habitat Joint Venture (RHJV 2004). We also included as many additional RHJV-designated riparian focal species as possible with adequate sample size. Only Blue Grosbeaks (scientific names for bird species analyzed are in the Appendix), among species not in the top 20, met the requirement of at least 100 detections. Bank Swallows (*Riparia riparia*) were detected in similar numbers to Blue Grosbeaks but the species is colonial and not reliably surveyed using point counts (Ralph et al. 1993, 1995). Thus, this species was not included. Twenty-one species were analyzed: 20 passerines species and Nuttall's Woodpecker (Appendix).

Treatment of Dependent Variables and Principal Components.—We calculated an abundance index for species by summing the number of detections per species over the three surveys in a year. We then analyzed ln(mean detections + constant), where the mean was calculated over all years and the constant was the smallest non-zero abundance value (Nur et al. 1999). Log-transformation of mean total detections per species was used because it yielded better predictive relationships with independent variables than use of untransformed mean detections and served to better normalize residuals. Residuals of the resultant models in all cases but one were approximately normally distributed (*sktest* procedure and examination of quantile-quantile plots for a normal distribution) (Nur et al. 1999, StataCorp. 2003). The exception was Bullock's Oriole, but log transformation was still preferred to no transformation. Analysis of log-transformed data is preferred if birds respond in a multiplicative manner to habitat factors, which is reasonable (i.e., with every unit increase in the independent variable, abundance increases by a fixed proportion or decreases by the same proportion) (Nur et al. 1999).

Mean values analyzed were based on a different number of years per point count station. Analyses were weighted by the square-root of the number of years of data (mostly 4 yrs/point, but in some cases 2 or 3 yrs) because the standard error of the mean detection per point is inversely proportional to the square-root of the number of years of data (Neter et al. 1990). Abundance values derived from fewer years of data contributed less to model results than those with more years of data. We conducted a principal component analysis (PCA) of the habitat variables to examine how well the 16 variables were represented by a smaller number of principal components (Legendre and Legendre 1998, Lichstein et al. 2002).

Model Selection and Statistical Analysis.—We used backward variable selection, considering each species one at a time, following Catchpole et al. (2004:15) for identifying the best statistical model. We started with 16 independent, quantitative variables for each species, plus region, treated as a categorical variable in the model (Sacramento, Cosumnes, or San Joaquin rivers). We used a two-stage model selection process (Zuur et al. 2007); first using a backward stepwise-procedure to choose the model with lowest Akaike Information Criterion (AIC) value. We then used a stepwise procedure to drop, one at a time, any additional variables from the AIC-preferred model that were not significant at the $P \leq 0.10$ level, using an F-test. This second stage was necessary because AIC is often over inclusive, selecting models that include nonsignificant variables, even at the $P < 0.1$ level. Model selection using AIC, especially with large sample sizes, leads to inclusion of extraneous (ecologically unrelated) variables (Brooks et al. 2000, Hansen and Yu 2001, Davison 2003: 404).

We considered an alternative approach, the Bayes Information Criterion (BIC; Schwarz 1978), which has been criticized for being too stringent (i.e., setting thresholds too high for including additional variables; Hansen and Yu 2001). The approach we used was intermediate between AIC alone and BIC.

We evaluated the consistency of the effect of each variable identified in the optimal statistical model for each species by testing for an interaction of that variable with region, while including other identified variables in the statistical model. We did not evaluate interactions of variables not included in the final species-specific model. We evaluated the significance of the specified interaction while including the second (or third) interaction in the model where more than one interaction was identified for a species at $P < 0.1$. We compared total R^2 and partial R^2 (Neter et al. 1990) for models that explain variation in abundance in relation to: (1) habitat variables only, (2) regional differences only (region treated as a categorical variable), and (3) both sets of variables, considered simultaneously.

The first three principal components from the habitat variable PCA were used to statistically model the response of individual species' abundance. We compared models using the 16 habitat variables with models using the first three principal components with respect to R^2 and partial R^2. We consider $P > 0.1$ to indicate lack of statistical significance and $P < 0.05$ to indicate statistical significance. We consider the results to be inconclusive where $0.05 < P < 0.10$, and report the P value.

RESULTS

Habitat Variables.—The overall 16-dimensional variation among independent variables was not well captured by a small number of easily interpretable principal components (Table 1). Sixty-one percent of the variance of the independent variables was accounted for by the first three principal components (proportion of the variance explained by each of the first 5 components was 0.301, 0.158, 0.151, 0.081, and 0.064, respectively).

The first component contrasted tree species richness with herb cover as those two variables loaded most strongly but in opposite directions. Thus, a survey station scored high on the first principal component if tree species richness was high and herb cover was low. The second component reflected Fremont cottonwood (*Populus fremontii*) tree cover more than any other variable. The third component loaded most strongly on willow tree cover, willow shrub cover, presence of water, and tree dbh index. The fourth component contrasted mugwort (*Artemisia douglasiana*) and willow shrub cover (both positive) with valley oak (*Quercus lobata*) tree cover (negative). The fifth component contrasted mugwort cov-

er (positive) with valley oak shrub cover and willow tree cover. Tree height index, tree cover, shrub species richness, and blackberry cover did not load strongly on any of the five components. The first three principal components were used in statistical analyses of predictors of species-specific abundance.

Species-specific Abundance Models in Relation to Vegetation and Region.—Number of detections for each species varied more than 10-fold with Spotted Towhee having the most detections and Blue Grosbeak the least (Appendix). Region was included in 17 of 21 species-specific preferred models, demonstrating variation in abundance due to region that could not be accounted for by differences due to habitat variables (Table 2). Regional differences were not apparent for House Finch, Tree Swallow, Nuttall's Woodpecker, or Bullock's Oriole. At least one habitat variable was retained for all species. Seventeen of the 21 species' models included at least three habitat variables and six species' models included at least six habitat variables (Brown-headed Cowbird, Red-winged Blackbird, House Wren, American Robin, Common Yellowthroat, and Western Wood-Pewee). Overall R^2 varied from 21 to 58% for most (17 of 21) species abundance models, but for two species overall R^2 was less than 20% (Bullock's Oriole and House Finch) and for two species overall R^2 was greater than 70% (Song Sparrow, Western Wood-Pewee).

Fifteen of the 16 habitat variables were included in at least one species model (Table 2). Grass cover was not included, either positively or negatively, for any species. Tree species richness was only included in models for two species (Spotted Towhee, negative; Bushtit, positive). Willow tree cover, was included only for House Wren. In contrast, willow shrub cover (i.e., which includes trees <5 m in height) was included in six species' models. Thirteen of the 16 variables were included in models for at least four species.

The three variables included in the most species models were herb cover (11 species), presence of water (9 species), and tree dbh index (8 species). Herb cover was often included, yet grass cover was not included. These two variables were the only two variables that tracked the herb stratum. Variables reflecting tree cover or tree size were often included in the models. These included species-specific tree variables as well as tree dbh index (8 species) and tree height index (7 species). Tree dbh index and tree height index were not included in the same model. The effect of tree size could be captured by one of the two indices, although which index depended on the species.

Most habitat variables had both positive and negative effects, depending on bird species. The two exceptions were blackberry and mugwort, for which only positive effects were demonstrated (5 and 4 species, respectively).

Variability in the Effect of Habitat and Vegetation Across Regions.—The majority of variables, when examined species by species, did not demonstrate heterogeneity of slopes among regions (Table 3). However, most variables (11 of 15 examined) demonstrated a significant interaction ($P < 0.05$) with region for at least one species. Four variables (tree cover, shrub cover, herb cover, and tree dbh index) had significant interactions for two bird species and none had significant interactions for more than two species.

Slopes differed quantitatively, not qualitatively, in eight cases (Table 3). In these instances, slopes for the variable in question were in the same direction (all positive or all negative) when examined region by region, but because the region-specific coefficients were sufficiently dissimilar, an interaction was detected (coded "1" in Table 3). The evidence in six cases indicated the effect of a variable was confined to a single region (coded "2"in Table 3) with no effect apparent in the other two regions. There were four cases where the estimated slopes differed quantitatively and qualitatively among regions (coded "3" in Table 3). Marked contrasts were observed for the effect of tree dbh index for Common Yellowthroats (significantly positive for Sacramento sites, but significantly negative slope for Cosumnes sites), and for cottonwood tree cover for Western Kingbirds (significantly positive for Sacramento sites, but significantly negative slope for San Joaquin sites). House Wrens had a significant positive effect for mugwort cover at Sacramento sites but an apparently negative effect ($P = 0.085$) at San Joaquin sites; Blue Grosbeaks had a significant negative effect for valley oak tree cover at Co-

TABLE 2. Species-specific statistical models for abundance of 21 species in relation to 16 habitat/vegetation variables in the Central Valley of California, controlling for region (Sacramento, Cosumnes, or San Joaquin). Species names in Appendix.

Variable	BHGR	BLGR	SPTO	ATFL	BHCO	RWBL	HOFI	HOWR	TRES	AMGO	SOSP	BUSH	WEKI	BEWR
Water presence			N**			N**			P++++	N***			P+	
Tree cover			P++				N****	N**					N****	
Shrub cover			P++++					N*		N**	P+++		N***	
Herb cover	N****				P+++	P++++		N****						N****
Tree species richness			N***									P++++		
Shrub species richness				P+++	N*									
Tree dbh index		N**	P++++		P++	N***								P++
Tree height index				P++++			P++++	P+++	P+++	P+++	N***			
Willow shrub cover	P++						N***	N****						
Willow tree cover								P+						
Cottonwood tree cover	P++							P+++	P++++	N**			P++	
Valley oak shrub cover		N*				P+++					N*			
Valley oak tree cover		N****			N**	N****		P++++	N**	N**		P+++		
Blackberry cover					P++	P++							P+	P+++
Mugwort cover					P+									
Grass cover														
Region in final model?	Yes	Yes	Yes	Yes	Yes	Yes	No	Yes	No	Yes	Yes	Yes	Yes	Yes
R^2 final model (%)	57.4	25.7	44.8	29.6	26.4	57.6	18.4	48.7	29.1	20.9	71.2	37.7	45.7	44.0
Vegetation/habitat variables in model (n)	3	3	5	2	6	6	3	8	4	5	3	2	5	3

N and * are negative, P and + are positive. * or + indicates $0.05 < P < 0.10$. ** or ++ indicates $0.05 < P < 0.01$. *** or +++ indicates $0.001 < P < 0.01$. **** or ++++ indicates $P = 0.001$ or less. Str (Strong) refers to $P < 0.01$; Mod (Moderate) refers to $0.01 \leq P < 0.10$.

TABLE 2. Continued.

Variable	AMRO	NUWO	BUOR	WESJ	LAZB	COYE	WEWP	Response summary				
								Totals	Str Neg	Mod Neg	Str Pos	Mod Pos
Water presence	P+++				N**	N***	P++	9	2	3	2	2
Tree cover				P++++		P+++		6	2	1	2	1
Shrub cover	N**						N***	7	2	3	2	0
Herb cover	N**	N****		P+	P++++	P++++	N****	11	5	1	4	1
Tree species richness								2	1	0	1	0
Shrub species richness				P+			N***	4	1	1	1	1
Tree dbh index	P++					P+++	P++++	8	1	1	3	3
Tree height index		P++++						7	1	0	6	0
Willow shrub cover				P++++	P+++	P+++		6	2	0	3	1
Willow tree cover								1	0	0	0	1
Cottonwood tree cover			P+			N***		7	1	1	2	3
Valley oak shrub cover	P++++							4	0	2	2	0
Valley oak tree cover								7	2	3	2	0
Blackberry cover	P++							5	0	0	1	4
Mugwort cover					P++++	P+++	P++	4	0	0	2	2
Grass cover								0	0	0	0	0
Region in final model?	Yes	No	No	Yes	Yes	Yes	Yes					
R^2 final model (%)	29.1	42.7	1.5	25.2	55.2	32.9	77.1					
Vegetation/habitat variables in model (n)	6	2	1	4	4	7	6					

N and * are negative, P and + are positive. * or + indicates $0.05 < P < 0.10$. ** or ++ indicates $0.05 < P < 0.01$. *** or +++ indicates $0.001 < P < 0.01$. **** or ++++ indicates $P = 0.001$ or less. Str (Strong) refers to $P < 0.01$; Mod (Moderate) refers to $0.01 \leq P < 0.10$.

TABLE 3. Interactions of 16 habitat variables with region for 20 species (Western Wood-Pewee omitted). Species names in Appendix.

Variable	BHGR	BLGR	SPTO	ATFL	BHCO	RWBL	HOFI	HOWR	TRES	AMGO	SOSP	BUSH	WEKI	BEWR	AMRO	NUWO	BUOR	WESJ	LAZB	COYE	Species examined	Species detected
Water presence						2***				1*											9	2
Tree cover			2***				1**														6	2
Shrub cover										2***	1**										7	2
Herb cover						1*												2**	2***		11	3
Tree species richness																					2	0
Shrub species richness				1**																	4	1
Tree dbh index						1****														3****	8	2
Tree height index											1**										7	1
Willow shrub cover																					6	0
Willow tree cover								2**													1	1
Cottonwood t. cover													3**								7	1
Valley oak shrub cover																					4	0
Valley oak tree cover		3**																			7	1
Blackberry cover																					5	1
Mugwort cover								3***											1*		4	2
Grass cover																					0	0
Interactions (n)	0	1	1	1	0	3	1	2	0	2	2	0	1	0	0	0	0	1	2	1		

* $0.05 < P < 0.10$; ** $0.01 < P < 0.05$; *** $0.001 < P < 0.01$; **** $P < 0.001$; 1 = all region-specific slopes in same direction; 2 = slopes differ in sign but only the slope(s) in one direction is (are) significant at $P < 0.10$; 3 = two region-specific slopes with opposite sign and both are significant at $P < 0.10$.

TABLE 4. Coefficients of determination and partial R^2 due to habitat variables only and to regional main effect only. No significant region main effects indicated by*.

Species	R^2 Full model	R^2 Model with habitat variables; no region	R^2 Model with region only	Partial R^2 due to habitat variable, for full model
Black-headed Grosbeak	0.574	0.400	0.413	0.161
Blue Grosbeak	0.257	0.009	0.15	0.107
Spotted Towhee	0.448	0.354	0.214	0.234
Ash-throated Flycatcher	0.296	0.038	0.143	0.153
Brown-headed Cowbird	0.264	0.194	0.168	0.096
Red-winged Blackbird	0.576	0.415	0.259	0.317
House Finch*	0.184	0.184	0	0.184
House Wren	0.494	0.366	0.179	0.315
Tree Swallow*	0.291	0.291	0	0.291
American Goldfinch	0.209	0.157	0.130	0.079
Song Sparrow	0.712	0.217	0.687	0.025
Bushtit	0.377	0.252	0.301	0.076
Western Kingbird	0.457	0.29	0.348	0.109
Bewick's Wren	0.44	0.423	0.036	0.404
American Robin	0.291	0.182	0.117	0.174
Nuttall's Woodpecker*	0.432	0.432	0	0.432
Bullock's Oriole*	0.015	0.015	0	0.015
Western Scrub-jay	0.252	0.205	0.128	0.124
Lazuli Bunting	0.552	0.354	0.454	0.098
Common Yellowthroat	0.329	0.086	0.108	0.221
Western Wood-Pewee	0.771	0.214	0.531	0.240

sumnes sites, but an apparently positive effect at San Joaquin sites ($P = 0.060$).

Variance in Bird Abundance Explained by Habitat Variables, Compared to Region.—We compared the magnitude of variance in abundance explained by habitat variables with that explained by region main effects for each of the 21 species, (Table 4). The R^2 in 13 cases was 20% or more and in 7 cases was 35% or more for habitat-only statistical models, excluding region main effects, (Table 4). The amount of variance explained by region differed even more among species than variance explained by habitat variables. There were four species for which region main effects, in the absence of habitat variables, accounted for 35% or more of the variance in species abundance: Song Sparrow, Western Wood-Pewee, Lazuli Bunting, and Black-headed Grosbeak. However, in two of the four cases (Lazuli Bunting and Black-headed Grosbeak), regional differences were reduced once habitat differences were controlled. Regional differences were paramount for Western Wood-Pewee and Song Sparrow, and consideration of habitat variables did not alter this finding. The effects of region were negligible for four species. The most anomalous species was Bullock's Oriole for which a habitat model could only explain 1.5% of the variance and region was not included.

The median partial R^2 due to habitat variables was 16%; for four species the partial R^2 due to habitat variables was over 30% (Red-winged Blackbird, Bewick's Wren, House Wren, Nuttall's Woodpecker). The median partial R^2 due to region effects was 12.5%; the partial R^2 due to region was over 30% for Song Sparrow and Western Wood-Pewee.

Species-specific Models Using Principal Components of Vegetation and Habitat Features.—We compared the performance of models for the 21 species using the first three principal components (extracted from the 16 habitat variables; Table 1) with models using individual habitat variables (Table 2). At least one of the first three principal components was at least moderately associated ($P < 0.10$) with the abundance index in a model that included region main effects for each species with the exception of Brown-headed Cowbird, Song Sparrow, and Common Yellowthroat (Table 5). The P-values for those three species associated with the best-fitting principal com-

TABLE 5. Coefficients of determination for models with region and first three principal components of habitat variables. Results are shown for models with retained principal components[a]. Partial R^2, after controlling for region, is shown for principal component model and for individual habitat variables.

Species	R^2 for model with region and principal component(s)[a]	Partial R^2 due to principal component(s)[b]	Partial R^2 due to individual habitat variables	Principal components retained[c]
Black-headed Grosbeak	0.519	0.106	0.161	I
Blue Grosbeak	0.186	0.036	0.107	I
Spotted Towhee	0.382	0.168	0.234	I
Ash-throated Flycatcher	0.237	0.094	0.153	I
Brown-headed Cowbird	0.170	0.002	0.096	(II)
Red-winged Blackbird	0.531	0.272	0.317	I, III
House Finch*	0.056	0.056	0.184	I
House Wren	0.343	0.164	0.315	I, II
Tree Swallow*	0.126	0.126	0.291	I, II, III
American Goldfinch	0.145	0.015	0.079	II
Song Sparrow	0.700	0.013	0.025	(II)
Bushtit	0.359	0.058	0.076	I
Western Kingbird	0.376	0.028	0.109	I
Bewick's Wren	0.348	0.312	0.404	I, III
American Robin	0.171	0.054	0.174	I
Nuttall's Woodpecker*	0.378	0.378	0.432	I, II
Bullock's Oriole*	0.005	0.005	0.015	III
Western Scrub-jay	0.157	0.029	0.124	I
Lazuli Bunting	0.495	0.041	0.098	I
Common Yellowthroat	0.116	0.008	0.221	(I)
Western Wood-Pewee	0.752	0.221	0.240	I, II, III

[a] Principal component retained if $P < 0.1$ in model with region; or if no component $P \leq 0.1$, then the one with lowest P value.
[b] Model includes region main effects, except for asterisked species.
[c] Principal component I, II, and/or III retained; shown in parentheses if $P > 0.1$.

ponent was $P > 0.2$ in each case. PC I (Table 1) was included in the final principal-component model for sixteen species, PC II was included for five species, and PC III was included for five species. The partial R^2 due to individual habitat variables, after controlling for region main effects, was greater, and usually much greater, compared to the partial R^2 due to the retained principal components (Table 5). Partial R^2 due to habitat variables for eight species was at least three times that of partial R^2 due to the principal components; partial R^2 due to habitat variables for seven species was between 50 and 150% greater than that due to principal components.

DISCUSSION

Importance of Habitat Differences at the Local Scale.—Variation in abundance of riparian-associated songbird species in the Central Valley of California was strongly associated with local-scale vegetation characteristics for each species examined, except one. Only for Bullock's Oriole was abundance not explained well by any habitat variable. Variables in the statistical models included both species-specific variables (e.g., cottonwood cover or mugwort cover) as well as more general variables (shrub cover or tree height index). Wiens and Rotenberry (1981) reported that vegetation composition was more predictive of bird abundance in shrub-steppe habitat than were measures of habitat structure (physiognomy).

Our findings emphasize the importance of including species-specific vegetation composition in analyses of habitat features influencing bird species presence or abundance. There is extensive literature reporting on habitat-associations for terrestrial bird species (Verner et al. 1986, McCullough and Barrett 1992, Scott et al. 2002), but most studies have analyzed general habitat characteristics and not species-specific vegetation composition, as exemplified by Block et al. (1986), Larson and Bock (1986), Sanders and Edge (1998), Sallabanks et al. (2000), Vernier et al. (2002), and Miller et al. (2004).

The omission of potentially important vegetative characteristics has implications for studies that contrast the importance of local habitat features with that of landscape-scale features in predicting species-specific patterns of avian abundance or presence. Lichstein et al. (2002) and Miller et al. (2004) summarize recent studies, which have generally been mixed: some indicate that local scale is more important than landscape scale and others have come to the opposite conclusion. The problem of insufficient characterization of vegetation may explain the different conclusions reached by Saab (1999) and Scott et al. (2003), both of which focused on riparian songbirds in the Idaho/Montana region. The former concluded that landscape variables were more important than local variables, while the latter concluded that local variables were more important. However, only Scott et al. (2003) included understory vegetation in the analysis.

Specific Vegetation Features of Importance to Birds.—The two variables that were most often included with a positive effect on species-specific abundance were both measures of tree size: tree height index and tree dbh index. We also demonstrated that shrubs and, more specifically, understory vegetation, were predictive of the abundance of the 21 study species. This result is of interest as many studies of habitat associations for riparian songbirds have only examined plant species composition with regard to trees (e.g., Strong and Bock 1990, Saab 1999). Robertsen et al. (2002) also identified several songbird species in mixed forest habitat that responded to understory vegetation. Krueper et al. (2003) found that removal of cattle benefited riparian understory, which in turn influenced bird abundance.

Regional Variation and Spatial Scale.—We found marked variation in abundance among regions within a single, large watershed (Sacramento/San Joaquin Valley). All sites were within a single habitat classification ("valley-foothill riparian"), but a large amount of variation remained in bird species abundance attributable to region alone, after controlling for differences in vegetation composition.

Important differences in the effect of habitat variables were revealed across regions, similar to the findings of Heath and Ballard (2003). In some cases, birds in one region do not appear to respond to the same habitat variable as conspecifics in another region, but in a few cases responses appeared to differ qualitatively from one region to another. The causal basis for this heterogeneity is not clear. Site to site variation may reflect the rarity of a plant species; for example, a bird species may be selecting habitat that contains that plant species if the species is rare, but avoiding the habitat if the plant species is common. Associations among plant species may also differ by region. For example, at the Cosumnes sites, presence of valley oak trees was associated with continuous valley oak forest cover; valley oak trees in other locations were often a component of a mixed forest type including cottonwoods, walnuts (*Juglans* spp.), or black willow (*Salix nigra*). Thus, the presence of a species (such as valley oak) implied a different set of associated plants, depending on region.

The influence of particular habitat variables also depends on spatial scale (Heath and Ballard 2003). This scale-dependence was well illustrated by studies in shrub-steppe birds; Rotenberry and Wiens (1980) demonstrated the importance of general habitat-structural variables at a large (continental) scale, but Wiens and Rotenberry (1981) demonstrated the greater importance of vegetational, species-specific composition at a more local (single-region) scale.

Response of Birds to Multivariate Factors.—Some studies have analyzed the effects of habitat variables using ordination to reduce a rich multivariate data set of independent variables to a few factors, for example, by using principal components or non-metric multidimensional scaling and analyzing bird response to multivariate factors (Lichstein et al. 2002). Our results raise concern about this practice. The factors or axes so obtained may concisely capture a large portion of variation with respect to vegetation and habitat among study sites (Legendre and Legendre 1998), but there is no assurance these axes reflect a coherent set of elements to which birds respond. An example of this problem was evident for Common Yellowthroat where the individual variable model performed well, but the principal component model did not (partial $R^2 = 0.221$ vs. 0.008). Two of the variables from the in-

dividual variable model (tree cover and herb cover) for this species loaded moderately strongly on principal component I, but with opposite signs. However, in the individual variable model, the coefficients for both variables were positive. Thus, Common Yellowthroats were more abundant where tree cover and herb cover were both high, but because the first principal component weighted these two variables with opposite signs, their effects tended to cancel out in the principal component statistical model. Other studies have also demonstrated stronger correlations between bird abundance and individual variables than with principal component or other multivariate factors (Wiens and Rotenberry 1981, Ambuell and Temple 1983).

Limitations of the Study.—We did not analyze differences in detection of birds due to habitat differences. We restricted detections to a distance of 50 m to reduce this problem (Ralph et al. 1993), but even within this distance there could be salient differences in detection which would be confounded with differences in abundance. All points surveyed were within a single, broad habitat type and this might be expected to reduce differences in detection rate within our sample.

One should be cautious in inferring causation from patterns of association among bird and habitat variables unless one analyzes bird response to a change in habitat characteristics (which we have not done). Each variable identified in a species-specific model (Table 2) has statistical support for its inclusion, but we recognize the ubiquity of model uncertainty (Burnham and Anderson 2002). Recently developed data-mining techniques, such as classification and regression trees (Hastie et al. 2001) are likely to be of great heuristic value, especially when one is analyzing 21 different dependent variables.

We restricted our analyses to species that were moderately abundant to improve statistical power. We may have failed as a result to capture characteristics of uncommon species. For example, some avian components of the ecosystem we investigated have been extirpated or drastically reduced within human history (e.g., Yellow-billed Cuckoo [*Coccyzus americanus*], Yellow Warbler [*Dendroica petechia*], and Bell's Vireo [*Vireo bellii*]), and we were unable to create habitat models for them. It is possible the habitat features they require are drastically reduced or even absent within the region.

CONSERVATION IMPLICATIONS

Nearly all species studied were shown to respond predictably to local variation in vegetation and habitat, at the scale of a territory or home range. Obtaining information on vegetation composition is labor-intensive and requires in-the-field data collection; one cannot rely on remotely-sensed data. The second implication is that one cannot rely on a few focal species to capture the diverse response of the full set of species of interest (Chase et al. 2000, Chase and Geupel 2005). Conservation planners and managers must consider a large, diverse set of target species. The final implication is that recommendations and models need to be developed on a region-by-region basis, especially if one is drawing inferences based on patterns of correlation alone.

ACKNOWLEDGMENTS

Funding was provided by the California Bay-Delta Authority (principally Contract ERP 02-P17), David and Lucile Packard Foundation, The Nature Conservancy, USDI Fish and Wildlife Service, William and Flora Hewlett Foundation, Morgan Stanley Dean Whitter & Co., the National Fish and Wildlife Foundation, and the National Science Foundation (DBI-0542868). We thank numerous PRBO project leaders, field biologists, and intern biologists, especially Anne King, Ryan Degaudio, Tonya Haff, Stacy Small, and Mike Lynes. We thank Mike Eaton, Ramona Swenson, Joe Silveira, Ramon Vega, Tara Zimmerman, Dawit Zeleke, Dennis Woolington, Valerie Calegari, and Becky Waegell, for support. We thank Tom Gardali, Viola Toniolo, Chrissy Howell, and Mike Green for helpful comments and other assistance and especially Greg Golet for support and insightful comments. This is PRBO Contribution Number 1618.

LITERATURE CITED

Abell, D. L. (Editor). 1989. Proceedings of the California Riparian Systems Conference: protection, management, and restoration for the 1990's. USDA, Forest Service, General Technical Report PSW-110. Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

Ambuell, B. and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057–1068.

Block, W. M., L. A. Brennan, and R. J. Gutiérrez. 1986. The use of guilds and guild-indicator species for assessing habitat suitability. Pages 109–

113 *in* Wildlife 2000: modeling habitat relationships of terrestrial vertebrates (J. Verner, M. L. Morrison, and C J. Ralph, Editors). University of Wisconsin Press, Madison, USA.

Brooks, S. P., E. A. Catchpole, B. J. T. Morgan, and S. C. Barry. 2000. On the Bayesian analysis of ring-recovery data. Biometrics 56:951–956.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second Edition. Springer Verlag, New York, USA.

Catchpole, E. A., Y. Fan, B. J. T. Morgan, T. H. Clutton-Brock, and T. Coulson. 2004. Sexual dimorphism, survival and dispersal in red deer. Journal of Agricultural, Biological, and Environmental Statistics 9:1–26.

Chase, M. and G. R. Geupel. 2005. The use of avian focal species for conservation planning in California. Pages 130–142 *in* Bird conservation implementation and integration in the Americas: Proceedings of the Third International Partners in Flight Conference (C. J. Ralph and T. D. Rich, Editors). USDA, Forest Service, General Technical Report PSW-GTR-191. Pacific Southwest Forest and Range Experiment Station, Albany, California, USA.

Chase, M. K., W. B. Kristan III, A. J. Lynam, M. V. Price, and J. T. Rotenberry. 2000. Single species as indicators of species richness and composition in California coastal sage scrub birds and small mammals. Conservation Biology 14:474–487.

Cody, M. L. 1985. Habitat selection in birds. Academic Press, Orlando, Florida, USA.

Davison, A. C. 2003. Statistical models. Cambridge University Press, Cambridge, United Kingdom.

Faber, P. (Editor). 2003. Proceedings of the riparian habitat and floodplains conference. Riparian Habitat Joint Venture, Sacramento, California, USA.

Hansen, M. H. and B. Yu. 2001. Model selection and the principle of minimum description length. Journal of the American Statistical Association 96: 746–774.

Hastie, T., R. Tibshirani, and J. Friedman. 2001. The elements of statistical learning: data mining, inference, and prediction. Springer Verlag, New York, USA.

Heath, S. K. and G. Ballard. 2003. Patterns of breeding songbird diversity and occurrence in riparian habitats of the eastern Sierra Nevada. Proceedings of the riparian habitat and floodplains conference (P. Faber, Editor). Riparian Habitat Joint Venture, Sacramento, California, USA.

Hildén, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2:53–75.

Howell, C. A., S. C. Latta, T. M. Donovan, P. A. Porneluzi, G. R. Parks, and J. Faaborg. 2000. Landscape effects mediate breeding bird abundance in midwestern forests. Landscape Ecology 15:547–562.

Katibah, E. F. 1984. A brief history of riparian forests in the Central Valley of California. Pages 23–29 *in* California riparian systems: ecology, conservation, and productive management (R. E. Warner and K. M. Hendrix, Editors). University of California Press, Berkeley, USA.

Knopf, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105–111 *in* Riparian ecosystems and their management: reconciling conflicting uses (R. R. Johnson, C. D. Ziebell, D. R. Patten, P. F. Folliot, and R. H. Hamre, Editors). USDA, Forest Service, General Technical Report RM-120. Rocky Mountain Station, Fort Collins, Colorado, USA.

Krueper, D., J. Bart, and T. D. Rich. 2003. Response of vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona (U.S.A.). Conservation Biology 17:607–615.

Lack, D. 1933. Habitat selection in birds, with special reference to the effects of afforestation on the Breckland avifauna. Journal of Animal Ecology 2: 239–262.

Larson, D. L. and C. E. Bock. 1986. Determining avian habitat preferences by bird-centered vegetation sampling. Pages 37–43 *in* Wildlife 2000: modeling habitat relationships of terrestrial vertebrates (J. Verner, M. L. Morrison, and C. J. Ralph, Editors). University of Wisconsin Press, Madison, USA.

Legendre, P. and L. Legendre. 1998. Numerical ecology. Second English Edition. Elsevier, Amsterdam, The Netherlands.

Lichstein, J. W., T. R. Simons, and K. E. Franzreb. 2002. Landscape effects on breeding songbird abundance in managed forests. Ecological Applications 12:836–857.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

Mayer, K. E. and W. F. Laudenslayer (Editors). 1988. A guide to wildlife habitats of California. California Department of Fish and Game, Sacramento, USA.

McCullough, D. R. and R. H. Barrett (Editors). 1992. Wildlife 2001: populations. Elsevier Applied Science, New York, USA.

Miller, J. R., M. D. Dixon, and M. G. Turner. 2004. Response of avian communities in large-river floodplains to environmental variation at multiple scales. Ecological Applications 14:1394–1410.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs. Third Edition. Irwin Press, Homewood, Illinois, USA.

Nur, N., S. L. Jones, and G. R. Geupel. 1999. Statistical guide to data analysis of avian monitoring programs. Biological Technical Publication BTP-R6001-1999. USDI, Fish and Wildlife Service, Washington, D.C., USA.

Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Monitoring bird populations by point counts. USDA, Forest Service, General Technical Report PSW-GTR-149. Pacific Southwest Forest and Range Experiment Station, Albany, California, USA.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. USDA, Forest Service, General Technical Report PBSD-GTR-144. Pacific Southwest Forest and Range Experiment Station, Albany, California, USA.

Riparian Habitat Joint Venture (RHJV). 2004. Version 2.0. The riparian bird conservation plan: a strategy for reversing the decline of riparian associated birds in California. Available from http://www.prbo.org/calpif/plans.html.

Rich, T. D. 2002. Using breeding land birds in the assessment of western riparian systems. Wildlife Society Bulletin 30:1128–1139.

Robertsen, M. J., S. A. Temple, and J. Coleman. 2002. Predicting the distribution of songbirds in forests of central Wisconsin. Pages 399–410 *in* Predicting species occurrences (J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Hauffer, M. G. Raphael, W. A. Wall, and F. B. Sampson, Editors). Island Press, Washington, D.C., USA.

Rotenberry, J. T. and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

Saab, V. A. 1999. The importance of spatial scale to habitat use by breeding birds in cottonwood forests: a hierarchical analysis. Ecological Applications 9:135–151.

Sallabanks, R., J. R. Walters, and J. A. Collazo. 2000. Breeding bird abundance in bottomland hardwood forests: habitat, edge, and patch size effects. Condor 102:748–758.

Sanders, T. A. and W. D. Edge. 1998. Breeding bird community composition in relation to riparian vegetation structure in the western United States. Journal of Wildlife Management 62:461–473.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics 6:461–464.

Scott, J. M., P. J. Heglund, M. L. Morrison, J. B. Hauffer, M. G. Raphael, W. A. Wall, and F. B. Sampson (Editors). 2002. Predicting species occurrences. Island Press, Washington, D.C., USA.

Scott, M. L., S. K. Skagen, and M. F. Merigliano. 2003. Relating geomorphic change and grazing to avian communities in riparian forest. Conservation Biology 17:284–296.

StataCorp. 2003. Stata statistical software. Release 8.0. Stata Corporation, College Station, Texas, USA.

Strong, T. R. and C. E. Bock. 1990. Bird species distribution patterns in riparian habitats in southeastern Arizona. Condor 92:866–885.

Tewksbury, J. J., A. E. Black, N. Nur, V. A. Saab, B. D. Logan, and D. S. Dobkin. 2002. Effects of anthropogenic fragmentation and livestock grazing on Western riparian bird communities. Studies in Avian Biology 25:158–202.

Verner, J., M. L. Morrison, and C. J. Ralph (Editors). 1986. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, USA.

Vernier, P. R., F. K. A. Schmiegelow, and S. G. Cummings. 2002. Modeling bird abundance from forest inventory data in the boreal mixed-wood forests of Canada. Pages 559–571 *in* Predicting species occurrences (J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Hauffer, M. G. Raphael, W. A. Wall, and F. B. Sampson, Editors). Island Press, Washington, D.C., USA.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8:1–93.

Wiens, J. A. and J. T. Rotenberry. 1981. Habitat association and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21–41.

Willson, M. 1974. Avian community organization and community structure. Ecology 66:1211–1214.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. Analyzing ecological data. Springer Science, New York, USA.

APPENDIX. Common and scientific names of bird species analyzed and species code. Species identified by RHJV (2004) as riparian focal species and total detections by species at all point count stations (n = 184) shown.

Common name	Scientific name	Code	Riparian focal species	Total detections
Nuttall's Woodpecker	*Picoides nuttallii*	NUWO		475
Western Kingbird	*Tyrannus verticalis*	WEKI		581
Ash-throated Flycatcher	*Myiarchus cinerascens*	ATFL		630
Western Wood-Pewee	*Contopus sordidulus*	WEWP		335
Western Scrub-jay	*Aphelocoma californica*	WESJ		435
Brown-headed Cowbird	*Molothrus ater*	BHCO		1106
Red-winged Blackbird	*Agelaius phoeniceus*	RWBL		726
Bullock's Oriole	*Icterus bullockii*	BUOR		416
House Finch	*Carpodacus cassinii*	HOFI		572
American Goldfinch	*Carduelis tristis*	AMGO		415
Song Sparrow	*Melodia melospiza*	SOSP	×	757
Spotted Towhee	*Pipilo maculatus*	SPTO		1425
Black-headed Grosbeak	*Pheucticus melanocephalus*	BHGR	×	638
Blue Grosbeak	*Guiraca caerulea*	BLGR	×	111
Lazuli Bunting	*Passerina amoena*	LAZB		406
Tree Swallow	*Tachycineta bicolor*	TRES	×	680
Common Yellowthroat	*Geothlypis trichas*	COYE	×	403
Bewick's Wren	*Thryomanes bewickii*	BEWR		767
House Wren	*Troglodytes aedon*	HOWR		848
Bushtit	*Psaltriparus minimus*	BUSH		605
American Robin	*Turdus migratorius*	AMRO		208

Short Communications

The Wilson Journal of Ornithology 120(4):856–862, 2008

First Description of the Breeding Biology and Natural History of the Ochre-breasted Brush Finch (*Atlapetes semirufus*) in Venezuela

Luis Biancucci[1,2] and Thomas E. Martin[1]

ABSTRACT.—We provide the first description of the eggs, breeding biology, and natural history of the Ochre-breasted Brush Finch (*Atlapetes semirufus*). We found 37 nests over four breeding seasons (2004–2007) in Yacambú National Park, Venezuela. Nesting activity started in late April and continued until early June suggesting single-brooded behavior despite a typical tropical clutch size of two eggs ($\bar{x}$ = 1.89) that were laid on consecutive days. Egg mass averaged 3.38 g and 11.6% of adult female mass. The incubation and nestling periods averaged 14.9 and 10.5 days, respectively. Only females incubated and the percent time they spent incubating did not change between early and late incubation. Females brooded 42.7% of the time when nestlings were 2 days of age and 20.5% when 9 days of age. Both parents provisioned young at a low rate (3.9 trips/hr) and nestling growth rate (k = 0.45) was also slow. Nest predation rates were relatively high with daily mortality rates of 0.058 and 0.067 during incubation and nestling stages, respectively. *Received 31 January 2007. Accepted 18 February 2008.*

The Ochre-breasted Brush Finch (*Atlapetes semirufus*) is restricted to Colombia and Venezuela (Hilty and Brown 1986, Hilty 2003) with an altitudinal range of 1,600–3,500 m in Colombia and 600–2,700 m in Venezuela (Hilty and Brown 1986, Remsen and Graves 1995, Stotz et al. 1996, Hilty 2003). This species is protected in several national parks in both countries and does not present immediate conservation challenges (IUCN 2007). Despite being a common bird (Ridgely and Tudor 1994), its breeding biology and life history remain largely unknown.

The objectives of our paper are to: (1) provide data on previously unknown life history traits, and (2) add to the knowledge of the natural history and breeding biology of the Ochre-breasted Brush Finch. Data were collected by field and video observations at 37 nests in four consecutive breeding seasons from 2004 to 2007. The work was conducted in Yacambú National Park at the northern end of the Andes in Venezuela (09° 42′ N, 69° 42′ W) at 1,350–2,000 m elevation. The park is in a mountainous area and has primary cloud forest and a small area of secondary forest (Fierro-Calderón and Martin 2007). The latter is where Ochre-breasted Brush Finches occur most often.

OBSERVATIONS

Nests and Nest Placement.—We searched for nests from the beginning of March until early July each year using two methods: (1) behavioral observation of parents, and (2) systematic search (Martin and Geupel 1993). Systematic search implies a thorough inspection through all suitable nesting habitat. It was usually conducted after seeing a pair exhibiting nesting behavior.

Ochre-breasted Brush Finches were fairly common in our study site and were easily seen and heard, and typically occurred as pairs. Our study plots ranged in altitude from 1,350 to 2,000 m elevation; however, we only detected this species below 1,600 m. Nests were in disturbed habitats: trail sides and secondary growth forests in well-lighted, grassy or vine-covered environments. Nests were usually concealed in grasses, vines or bushes, between 0.2 and 3 m above ground. Foraging activity occurred in the same habitat.

Breeding Season.—The breeding season starts in March, when the dry season is ending, and lasts until July, in about the middle of the rainy season. The earliest nest was found on 21 March and contained two fresh eggs, based on candling. Breeding activity was highest in late April through late May (Fig. 1).

Gender Difference and Roles.—Gender of

[1] USGS, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA.

[2] Corresponding author; e-mail: luis.biancucci@gmail.com

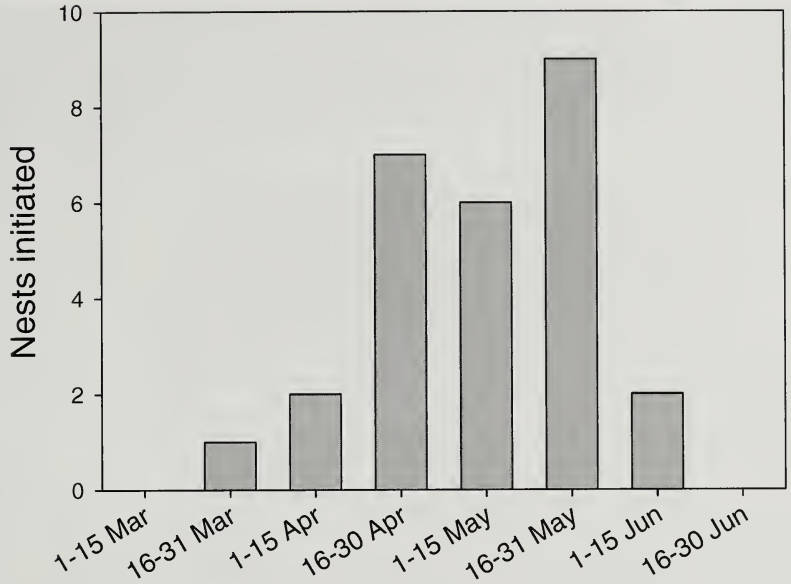


FIG. 1. Timing of bi-weekly nest initiation (n = 19) from early March to late June, 2004–2007 for Ochre-breasted Brush Finch at Yacambú National Park, Lara, Venezuela.

Ochre-breasted Brush Finches cannot be accurately assigned based on plumage. Roles of males and females during different periods of nesting were identified using behavior, video recording, and data from mist-netting. Pairs were together during nest building, but only one adult actually collected material and constructed the nest while the other bird followed and apparently guarded its mate. Only one adult incubated based on video recordings, and only females had developed brood patches among mist-netted birds. Thus, we assume that only the female builds the nest and incubates.

Nest Building and Laying.—The time the female used to build a nest and lay eggs varied throughout the breeding season. It usually took ~1 week to build a complete nest at the beginning of the season and another week to lay the first egg. A female took only 8 days to build a nest and lay a first egg towards the end of the season, after having lost her previous nest to predation.

The nest of *Atlapetes semirufus* is an open-cup usually built with thick grasses on the outside, at times complemented with small sticks on the outer edge. The lining consisted of thin grasses and rootlets. The inside color varies between yellow and brown, depending on materials used (Fig. 2).

We measured outer diameter (from edge to edge), inner diameter (cup), outer height (exterior bottom-to-top) and inner height (bottom-to-top of cup) of 29 nests. Nests averaged [± SE] 6.79 ± 0.12 cm in inner diameter, 12.59 ± 0.32 cm in outer diameter, 4.94 ± 0.13 cm in inner height, and 9.24 ± 0.32 cm in outer height.

Clutch Size and Eggs.—Clutch size was measured only for nests found during nest building or laying stages and was the number that did not change on subsequent days. Clutch size was two eggs in all but two nests and averaged [± SE] 1.89 ± 0.06 eggs (n = 28). Eggs were laid on consecutive days and were white with reddish-brown spots (Fig. 2). Spots were usually concentrated at the large end of the eggs, but may be more uniformly distributed; spots of a few eggs were faint and almost lacking. We weighed 24 eggs at 13 nests between day zero and day 3 of the incubation period using an ACCULAB portable electronic scale (precision 0.001 g). Fresh mass of eggs averaged [± SE] 3.38 ± 0.04 g. Adult male and female mass averaged 29.25 ± 0.33 g (n = 32) based on birds captured in mist nets throughout the breeding season. Thus, fresh egg mass represented 11.6% of the adult mass.

Incubation.—The incubation period was

FIG. 2. Nest and eggs of Ochre-breasted Brush Finch in Yacambú National Park. Photograph by A. M. Niklison.

measured as the number of days between the last egg laid and the last egg hatched (Briskie and Sealy 1990, Martin 2002). This period was measured only for nests found during the pre-laying or laying period and for which hatching day was observed. Nests were checked every other day, except at stage-changing events, such as start of incubation, hatching, and fledging, when nests were checked daily or twice daily. The mean [± SE] incubation period was 14.86 ± 0.26 days (n = 7). We assessed incubation behavior and nest attentiveness (percent of time adults spend on the nest incubating) by video filming nests for 6–8 hrs starting within 30 min of sunrise (Martin and Ghalambor 1999, Martin et al. 2007). Nests were filmed once during early and once during late incubation when possible. The mean duration of on- and off-bouts in early incubation was 34:17 and 15:34 (min:sec), respectively, and during late incubation was 44:49 and 15:24 (min:sec). Nest attentiveness averaged 69.4% (n = 1) on the third day of incubation, 70.6% (n = 1) in middle incubation (day 6), and 74.4% ± 0.35 (n = 3) during late incubation (last 4 days).

Nestling Period.—Hatching was synchronous in all nests of the Ochre-breasted Brush Finch. The nestling period length was 10.5 days (n = 2). Nestlings are able to jump from the nest when they feel threatened, at times as early as day 7, when their primary pin feathers are just breaking their sheaths (i.e., the day that feathers of the 8th primary break their sheaths). Brooding behavior (percent of time females spent brooding nestlings) and parental provisioning rates were measured using video recordings for 6–8 hrs beginning within 30 min of sunrise. Females brooded 42.7% (n = 1) of the time on day 2 of the nestling period and 20.5% (n = 1) of the time on day 9. Both males and females provision the young based on videos showing both adults at the nest simultaneously. The provisioning rate on day 2 of the nestling stage was 3.66 trips/hr (n = 1) and was similar on day 9 at 4.20 trips/hr (n = 1).

We measured tarsus length of nestlings using Mitutoyo digital calipers and body mass

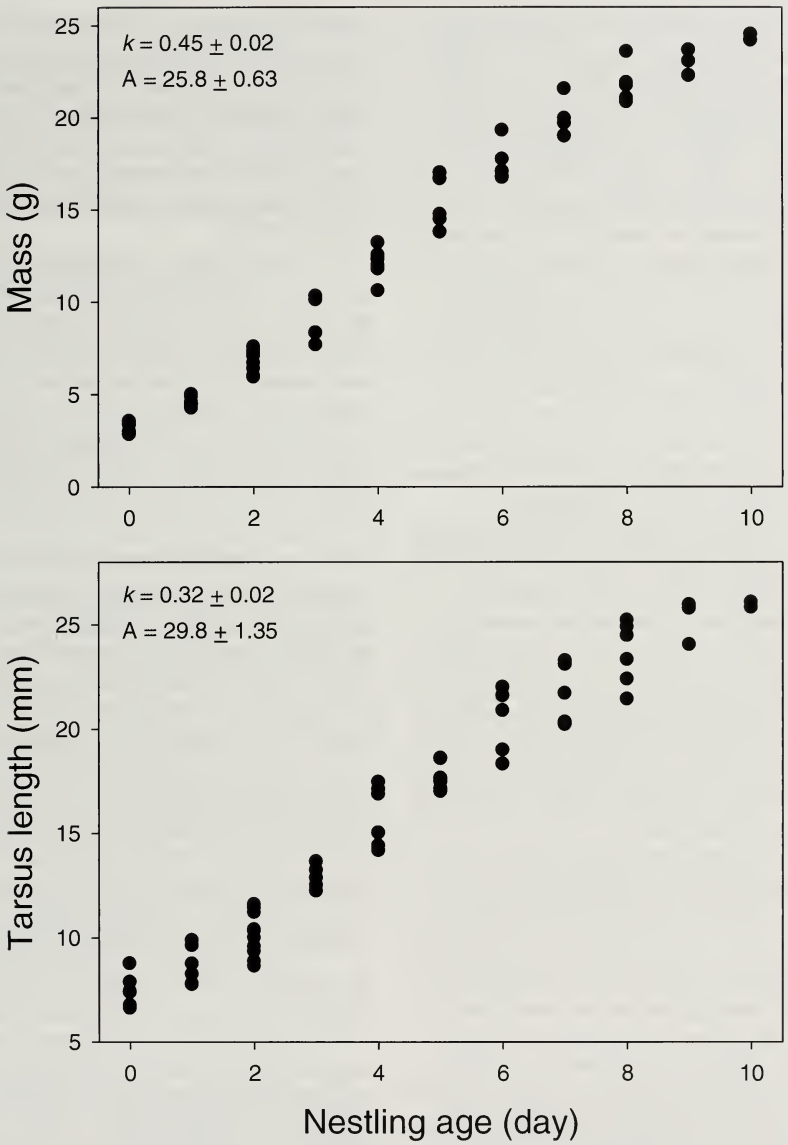


FIG. 3. Ochre-breasted Brush Finch nestling growth of mass and tarsus length with age. Growth rate constant (k) and asymptotic size (A) are indicated in each plot.

using ACCULAB digital electronic scales. Nestlings were measured every other day. We estimated growth rate following Remeš and Martin (2002) using the logistic growth function to estimate the growth rate constant (k) and asymptotic size (A). The estimated growth rate based on body mass was faster than when based on tarsus length (Fig. 3).

Nest Predation.—Predation accounted for all nesting mortality. We calculated daily nest predation rates using the Mayfield method (Mayfield 1975, Hensler and Nichols 1981). Daily predation rates ($\bar{x} \pm$ SE) were 0.070 ± 0.016 for the incubation period, 0.068 ± 0.025 for the nestling period, and 0.069 ± 0.013 (n = 37 nests; 378.5 exposure days) for the total nesting period including egg laying.

DISCUSSION

Ochre-breasted Brush Finches have an array of breeding features similar to those of congeneric species. Nest placement and shape

were similar to that of the Pale-headed Brush Finch (*A. pallidiceps*) (Oppel et al. 2003, 2004), White-naped Brush Finch (*A. albinucha)* (Cisneros Palacios 2005), and Yellow-striped Brush Finch (*A. citrinellus*) (Luis Biancucci, pers. obs.). The clutch size was within the range reported for the genus; clutch size for *A. albinucha* in Mexico was two eggs based on a single nest (Cisneros Palacios 2005), one to three eggs for *A. pallidiceps* in Ecuador (Oppel et al. 2003), one egg for *A. leucopis* (n = 1; Salaman et al. 1998), and two eggs for *A. citrinellus* in Argentina (n = 3; T. E. Martin, unpubl. data). Only the female in *A. pallidiceps* appeared to build the nest and incubate the eggs (Oppel et al. 2003), similar to our observations for *A. semirufus*.

Two closely related species, Chestnut-capped Brush Finch (*Buarremon brunneinucha*) and Stripe-headed Brush Finch (*B. torquatus*) also occur in our study site. The former usually prefers more forested habitat with good canopy cover. The latter nests in vines and bushes, but does not hide the nest between grass clumps as we observed for the Ochre-breasted Brush Finch. However, there is some nest site overlap between *Buarremon torquatus* and *A. semirufus* (Luis Biancucci, pers. obs.).

Our data are sparse but suggestive of a single brood per season; we did not observe birds attempting a second brood after a successful previous nest, and the season is sufficiently short that single-brooded behavior seems most likely. Single-brooded behavior was also observed for the closely-related Pale-headed Brush Finch (Oppel et al. 2003). This contrasts with most emberizines in North America, which are more commonly double-brooded (Martin 1995). The related genera, *Junco* and *Pipilo* (Klicka et al. 2000, Yuri and Mindell 2002, Carson and Spicer 2003) are both multi-brooded (Martin 1995). This pattern is opposite to the generally accepted view that tropical birds have more broods per season than north temperate relatives (Martin 1996).

The incubation period was similar to related tropical and subtropical species. The incubation period of the congener *A. pallidiceps* in Ecuador was 14 days (Oppel et al. 2003), similar to the 14.9 days that we found for *A. semirufus*. In Argentina, the Stripe-headed Brush Finch had an incubation period of 15.75 ± 0.17 days (Auer et al. 2007), and the Saffron-billed Sparrow (*Arremon flavirostris*) averaged 15.31 ± 0.25 days (Martin 2002, Auer et al. 2007). Related emberizine species in high elevation Arizona have shorter incubation periods: 12.6 days for Green-tailed Towhee (*Pipilo chlorurus*) and 12.4 days for Gray-headed Junco (*Junco hyemalis caniceps*) (Martin 2002).

Nest attentiveness was higher than for related species in Argentina where the same sampling protocols were used. The Stripe-headed Brush Finch averaged 54.8% and Saffron-billed Sparrow averaged 62.5% (Auer et al. 2007), while attentiveness averaged 71.5% for *A. semirufus*. Nest attentiveness of tropical species is commonly lower than north temperate relatives (Martin 2002, Chalfoun and Martin 2007), but the Ochre-breasted Brush Finch was similar to related species in Arizona; Green-tailed Towhee averaged 70.7% and Gray-headed Junco averaged 75.1% (Martin 2002). Nest attentiveness can affect length of the incubation period (Price 1998, Martin 2002, Martin et al. 2007), but cannot explain the difference in incubation period between *A. semirufus* and northern relatives.

The nestling period (10.5 days) was shorter than for Stripe-headed Brush Finch (12.75 ± 0.21 days) and Saffron-billed Sparrow (12.16 ± 0.24 days) in Argentina (Auer et al. 2007), but similar to related species in Arizona where it was 11.1 days for Green-tailed Towhee and 11.0 days for Gray-headed Junco (T. E. Martin, unpubl. data). Provisioning rates were about half the rate that parents fed nestlings in related species in Arizona based on the same sampling methods (Martin et al. 2000). Growth rates were slow compared with north temperate emberizines. For example, the growth rate constant based on mass was k = 0.45 ± 0.02 compared with 0.53 ± 0.01 for 31 north temperate emberizine species (Remeš and Martin 2002). This slow growth matches general expectations for tropical birds (Ricklefs 1968, 1976).

The Ochre-breasted Brush Finch has a smaller clutch size, longer incubation period, and lower provisioning rates than related north temperate species, as is common for tropical birds (Martin et al. 2000, 2007). However, the Ochre-breasted Brush Finch also exhibits several traits that are not typical of tropical birds and are more similar to north temperate relatives such as similar nestling period and nest attentiveness.

In contrast to conventional views (Martin 1996), it also appeared to have fewer broods than related north-temperate species despite a smaller clutch size and similar breeding season length. These data suggest that more work is needed on breeding biology of tropical birds to clarify perceived patterns of life history differences among latitudes.

ACKNOWLEDGMENTS

We thank A. M. Niklison and K. L. Decker for helpful comments on the manuscript, and several people for help in finding nests. This study was made possible in part by support under NSF grants DEB-9981527 and DEB-0543178 to T. E. Martin. Permit numbers are DM/0000237 from FONACIT, PA-INP-005-2004 from INPARQUES, and 01-03-03-1147 from Ministerio del Ambiente.

LITERATURE CITED

Auer, S. K., R. D. Bassar, J. J. Fontaine, and T. E. Martin. 2007. Breeding biology of songbirds in a subtropical montane forest in northwestern Argentina. Condor 109:321–333.

Briskie, J. and S. G. Sealy. 1990. Evolution of short incubation periods in the parasitic cowbirds, *Molothrus* spp. Auk 107:789–793.

Carson, R. J. and G. S. Spicer. 2003. A phylogenetic analysis of the emberizid sparrows based on three mitochondrial genes. Molecular Phylogenetics and Evolution 29:43–57.

Chalfoun, A. and T. E. Martin. 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. Animal Behavior 73:579–585.

Cisneros Palacios, E. 2005. First nesting record of White-naped Brush-finch (*Atlapetes albinucha*). Huitzil 6:6–7.

Fierro-Calderón, K. and T. E. Martin. 2007. Reproductive biology of the Violet-chested Hummingbird in Venezuela and comparisons with other tropical and temperate hummingbirds. Condor 109:680–685.

Hensler, G. L. and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42–53.

Hilty, S. L. 2003. Birds of Venezuela. Second Edition. Princeton University Press. Princeton, New Jersey, USA.

Hilty, S. L. and W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, USA.

International Union for the Conservation of Nature (IUCN). 2007. IUCN Red list of threatened species. www.iucnredlist.org (accessed 28 October 2007).

Klicka, J., K. P. Johnson, and S. M. Lanyon. 2000. New World nine-primaried oscine relationships: constructing a mitochondrial DNA framework. Auk 117:321–336.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101–127.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? Journal of Avian Biology 27:263–272.

Martin, T. E. 2002. A new view for avian life history evolution tested on an incubation paradox. Proceedings of the Royal Society of London Series B 269:309–316.

Martin, T. E. and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64: 507–519.

Martin, T. E. and C. K. Ghalambor. 1999. Males helping females during incubation. Required by microclimate or constrained by nest predation? American Naturalist 153:131–139.

Martin, T. E., S. K. Auer, R. D. Bassar, A. M. Niklison, and P. Lloyd. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. Evolution 61:2558–2569.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. Science 247:1482–1484.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Oppel, S., H. M. Schaefer, and V. Schmidt. 2003. Description of the nest, eggs, and breeding behavior of the endangered Pale-headed Brush-finch (*Atlapetes pallidiceps*) in Ecuador. Wilson Bulletin 115:360–366.

Oppel, S., H. M. Schaefer, V. Schmidt, and B. Schroder. 2004. Habitat selection by the Pale-headed Brush-finch (*Atlapetes pallidiceps*) in southern Ecuador: implications for conservation. Biological Conservation 118:33–40.

Price, T. 1998. Maternal and paternal effects in birds: effects on offspring fitness. Pages 202–226 *in* Maternal effects as adaptations (T. A. Mousseau and C. W. Fox, Editors). Oxford University Press, New York, USA.

Remeš, V. and T. E. Martin. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56:2505–2518.

Remsen, J. V. and W. S. Graves. 1995. Distribution patterns and zoogeography of *Atlapetes* Brush-finches (Emberizinae) of the Andes. Auk 112: 210–224.

Ricklefs, R. 1968. Patterns of growth in birds. Ibis 110:419–451.

Ricklefs, R. 1976. Growth rates of birds in the humid New World tropics. Ibis 118:179–207.

Ridgely, R. S. and G. Tudor. 1994. Birds of South America. Volume 2. University of Texas Press, Austin, USA.

Salaman, P. G. W., L. Dávalos, and G. M. Kirwan. 1998. The first breeding records of White-rimmed Brush-finch *Atlapetes leucopis* with ecological notes. Cotinga 9:24–26.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker, and D. K. Moskovits. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Yuri, T. and D. P. Mindell. 2002. Molecular phylogenetic analysis of Fringillidae, "New World nine-primaried oscines" (Aves: Passeriformes). Molecular Phylogenetics and Evolution 23:229–243.

The Wilson Journal of Ornithology 120(4):862–867, 2008

Reproductive Biology of the Red-ruffed Fruitcrow (*Pyroderus scutatus granadensis*)

James A. Muir,[1,2,3] Diane Licata,[1] and Thomas E. Martin[1]

ABSTRACT.—We provide a detailed report on the reproductive biology of the Red-ruffed Fruitcrow (*Pyroderus scutatus granadensis*). Eight nests were found between 2003 and 2007 in tropical montane cloud forest in Yacambu National Park, Lara, Venezuela. All nests were near streams in steep drainages. Nests consisted of twigs arranged in a cupped platform. Clutch size was a single egg and the average incubation period (n = 3) was 22.3 days. Nest attentiveness during incubation averaged [± SE] 76.3 ± 1.86% and increased only slightly across stages (early, middle, late). On-bout and off-bout durations were relatively similar across incubation stages. A nestling period of 35 days was recorded for one nest and feather pin-break was estimated to occur at day 19. Brooding attentiveness during the early nestling period averaged 62.5 ± 6.41%, and the adult ceased brooding at about feather pin-break. Food delivery rates increased with nestling age. Food provisioning consisted mostly of insects (66.7%) and lizards (25%) with fruit comprising only 8.3% of the nestling diet at early stages. Provisioning changed to mostly fruit (82.4%) and some insects (17.6%) in late stages of the nestling period. *Received 16 January 2007. Accepted 31 January 2008.*

The reproductive biology of endemic tropical birds is poorly known. Information on the life history of the Red-ruffed Fruitcrow (*Pyroderus scutatus*), despite having a broad neotropical distribution, is symptomatic of the poor knowledge of tropical endemics. *P. scutatus* is a locally rare and uncommon bird of the Cotinga family, a diverse family of passerines restricted to the Neotropics. Red-ruffed Fruitcrows are predominately frugivorous and inhabit mountainous regions of Venezuela, Colombia, Brazil, Paraguay, Peru, Ecuador, and Argentina. Most records and species accounts for *P. scutatus* are from Brazil and Colombia (Serrano 1994, Pizo et al. 2002). *Pyroderus scutatus granadensis* occurs in the Coastal Cordillera and lower Andean regions of Venezuela where it inhabits wet, humid, old growth forests (Hilty 2003). No comprehensive descriptions of the breeding biology of *P. scutatus granadensis* exist.

The Red-ruffed Fruitcrow is among the largest (300–390 g) passerines in the world (Snow 1982, Hilty 2003) and is considered rare within its range (Stotz et al. 1996). Consequently, life history data are essential for development of conservation strategies that may protect this species. The objectives of this paper are to describe aspects of the breeding biology of *P.scutatus* for the first time, and to discuss food provisioning during the nestling period. All data are from montane, wet, primary forest at Yacambu National Park, Lara State, Venezuela (09° 24′ N, 69° 30′ W; 1,750–2,000 m elevation). Data were collected from March through June 2002 through 2006.

OBSERVATIONS

Nest Locations and Descriptions.—We found eight nests of *P. scutatus granadensis* in tall forest areas of steep-sided river valleys and adjacent ridgelines within primary forest

[1] USGS, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA.

[2] Current address: Ensis, Biodiversity Division, Forestry Road, University of Canterbury, Christchurch, New Zealand.

[3] Corresponding author; e-mail: muir.j.a@gmail.com

(canopy height = ~35 m). Nests were found by thoroughly searching throughout the forest or by following adults to the nest site. The eight nests were all on the edge of streams. This is congruent with the description of three lek sites and six nest sites in a river drainage with steep-sided valleys at Ucumari National Park, Colombia (Serrano 1994). Our study sites ranged in elevation from 1,400 to 2,000 m. Red-ruffed Fruitcrows were observed and nests located in higher elevation plots (1,650–1,850 m). Seven of the eight nests that we found occurred within an area of ~6 ha in a major river drainage; the same general area was used for nesting among years. The earliest nest building behavior was observed on 27 March and the last was on 26 May. Most breeding activity appeared to occur during April, May, and June.

Nest heights were visually estimated between 3.5 and 11 m in mid-canopy trees (5–14 m in height). Three nests were in trees (*Solanum* spp.), one was in a tree fern (Cyatheaceae), and the remainder were in unknown tree species. Nests in *Solanum* spp. were placed in horizontal, forked, mossy branches in positions where leaves provided substantial cover for the nest.

Nests were large, untidy structures consisting of leafless twigs forming a shallow cup. On one occasion an individual brought sticks to the nest while another adult observed the nest from nearby. All other observations of nest building efforts were of solitary individuals. We prepared a detailed description of one nest. The nest was circular to elliptical in shape with an external diameter of 21.5–22.5 cm and an inner diameter of 14.8–15.6 cm. It was close to the trunk of the tree and supported by one main branch with a few large sticks spanning the gap to other branches. The main branch had a diameter of 3.0 cm. The nest was composed of two types of sticks. The outer part of the nest was composed of ~45 large, dark brown, dead sticks arranged to form a platform; the sticks were 30–60 cm long and averaged 4–5 mm in diameter. Some sticks had lichen, moss, or black rootlets growing on them. The inner sticks were light reddish-brown and flexible. The longest pieces were 25 cm in length, but most were ~10 cm with a diameter of 1–1.5 mm. The flexible sticks were woven to form a distinct cup placed on and woven into the large stick platform. The cup was tightly woven and more dense on the side closest to the tree trunk; it was not possible to see through it. The other side was more loosely woven. Nests measured in Colombia had an external diameter of 37.0 ± 7.5 cm and were lined with leaves (Serrano 1994, Snow 2004). The nest that we measured differed in external diameter and had no inner lining of leaf litter.

Clutch Size and Nest Success.—Each active nest had one egg. Six of eight nests were depredated; four during incubation and two during the nestling stage. One nestling fledged from one nest and the other nest was still active with a 20-day old nestling when we stopped monitoring at the end of June. Overall daily mortality (±SE) rate at these eight nests calculated using the Mayfield method was 0.032 ± 0.013 (exposure days = 190) (Hensler and Nichols 1981).

Laying and Incubation Behavior.—Red-ruffed Fruitcrows delayed laying eggs following nest completion; the time between nest completion and laying was 8 days at one nest checked daily and 6–8 days at two other nests. We measured incubation periods as the number of days between the last egg laid and last egg hatched (Briskie and Sealy 1990) based on visual inspection of nests. One of three nests where both laying and hatching were observed had an incubation period of 21 ± 1 day and two had an incubation period of 23 ± 1 day each.

Nest attentiveness (percent time spent on the nest incubating eggs) during incubation was measured by video-taping nests at early (day 1 to 3 of the incubation period), middle (day 8 to 13 of the incubation period), and late (day 17–22 of the incubation period) stages. The camera ran for 6–8 hrs and started within 1 hr of sunrise (Ghalambor and Martin 2001, Martin 2002). Only the female incubated, as males were not recorded attending the nest. Nest attentiveness remained similar across stages with a slight increase through incubation (Fig. 1A). Nest attentiveness averaged 76.3 ± 1.86% (n = 13) across all nests and stages. Duration of incubation on-bouts was similar across stages of the incubation period and averaged 60.0 ± 5.51 min (n = 13) across all nests and periods (Fig. 1B). Off-bout duration also was similar among periods (Fig.

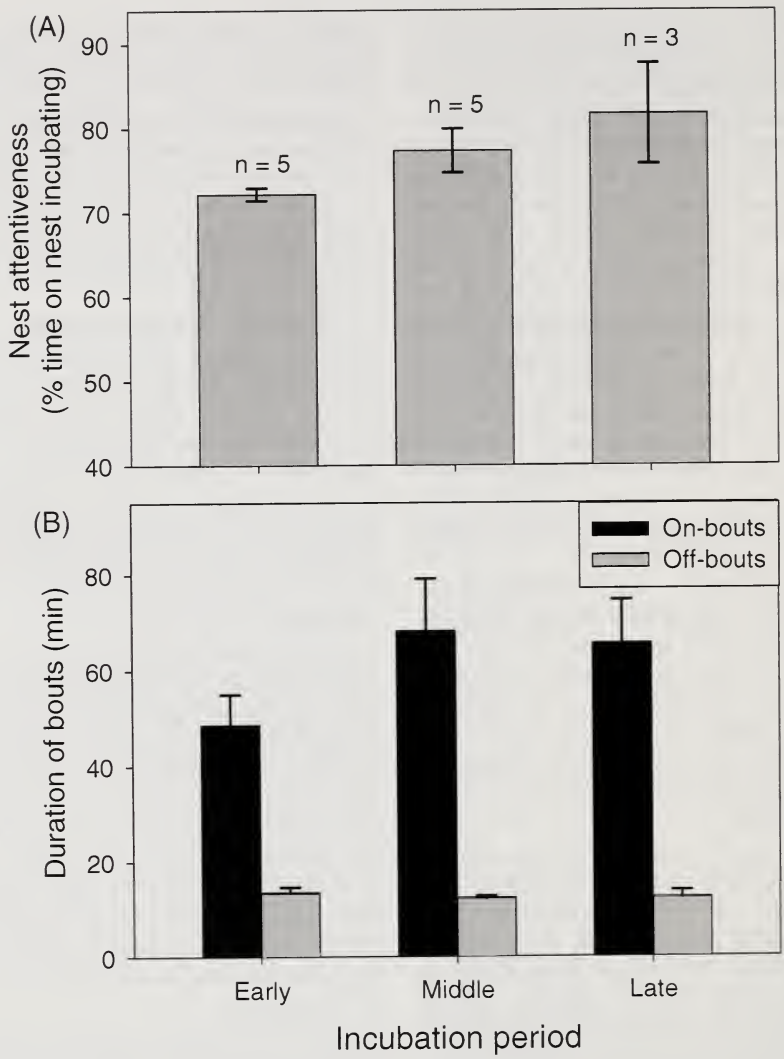


FIG. 1. Behaviors during early (day 1–3), middle (day 8–13), and late (day 17–22) stages of the incubation period for the Red-ruffed Fruitcrow: (A) nest attentiveness and (B) duration of on and off-bouts. Sample sizes (*n*) represent numbers of nests sampled and error-bars represent ± SE.

1B) and averaged 13.4 ± 0.59 min (n = 13) across all nests and periods.

Nestling Development.—Nestling development was documented by video taping a single nest in 2004. The nestling remained covered in thin feathery yellow-orange down from day 2 through day 15. Black feathers first developed on the wings, and pin feathers broke their sheaths about day 19 (±1 day) of the nestling period. The nestling had lost almost all of the down by day 21 and was standing and flapping in the nest. Only residual down remained on the eyebrow region by day 24 and the nestling had a well developed bill. The nestling at day 31 had adult-like black plumage and was about three quarters the size of the adult; the 'Red Ruff' throat plumage that is most distinctive in adults was extremely faint and almost non existent in the nestling at this stage. Serrano (1994) noted the 'Red Ruff' does not develop until the fledgling is 2 months of age. Video analysis indicated the nestling did not appear to vocalize and begging displays were infrequent and subdued. Serrano (1994) reported a soft 'mooing' vocalization between adult and nestling. We fol-

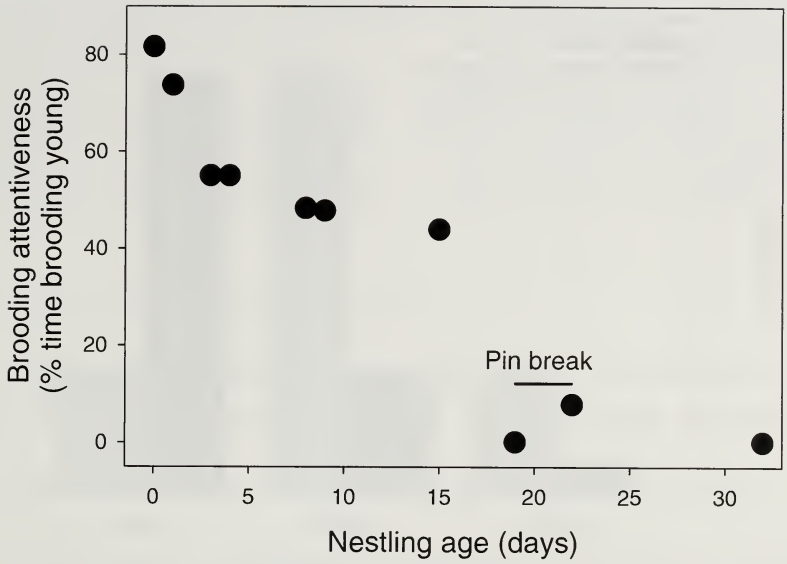


FIG. 2. Brooding attentiveness of the Red-ruffed Fruitcrow as a function of age of the nestling based on repeated video observations at two nests.

lowed one nest through to fledging with a nestling period of 35 days.

Brooding attentiveness (percent time spent brooding the nestling) during the nestling period was recorded by video-taping two nests starting on day 0 (hatching) and repeated once a week for 6–8 hrs per recording event. Brooding attentiveness decreased with age of the nestling and appeared to stop about the time of feather pin-break (Fig. 2). Adults provisioned nestlings an average of 0.18 ± 0.42 times/hr with little variation by age, varying from 0.14 to 0.22 visits/hr across stages.

Nestling Diet.—Food items brought by parents for nestlings were identified by viewing videos in two nests filmed at early (day 0–16), middle (day 17–22), and late (day 23–35) nestling stages. The diets of both nestlings were combined to characterize food type (Fig. 3). Food type was recorded if it was positively identifiable and was used to estimate the relative abundance of foods brought to nestlings at different ages. The incidence of fruit in the nestling's diet increased strongly from early to middle to late nestling stages (Fig. 3). Correspondingly, the incidence of insects in the nestling's diet decreased from early to late in the nestling stages (Fig. 3).

DISCUSSION

Male Red-ruffed Fruitcrows form communal leks (Hilty 2003) and do not help with parental care at any stage, leaving females to raise the young alone. Many species with female-only nest care are frugivorous or nectivorous (Beehler 1986, Cockburn 2006). A coevolutionary interaction between food plant and avian disperser has been proposed by Snow (1976) to be a causal factor influencing male emancipation from nesting duties (Beehler 1986, Cockburn 2006). Snow (1976) uses the Cotingas as exemplary subjects because the female appears to rear the nestling on lipid rich lauraceous fruits unassisted by the male. However fruit may not provide sufficient protein to allow rapid growth (Morton 1973). Data presented here and by Serrano (1994) indicate Fruitcrow nestlings do not have a significant fruit diet until late in the nestling period. Serrano (1994) reported that nestlings were fed only insects until day 10 of the nestling period and only fruit thereafter. In our study, insects were part of the nestling's diet throughout the nestling period in decreasing amounts with nestling age. The high protein diet of *P. scutatus* nestlings does not yield rapid growth but may be essential for development. Brietwisch et al. (1984) reported that nestling frugivory only becomes profitable as nestlings develop endothermy. *P. scutatus* adults may feed nestlings an optimal mixture of animal protein for growth, and fruit car-

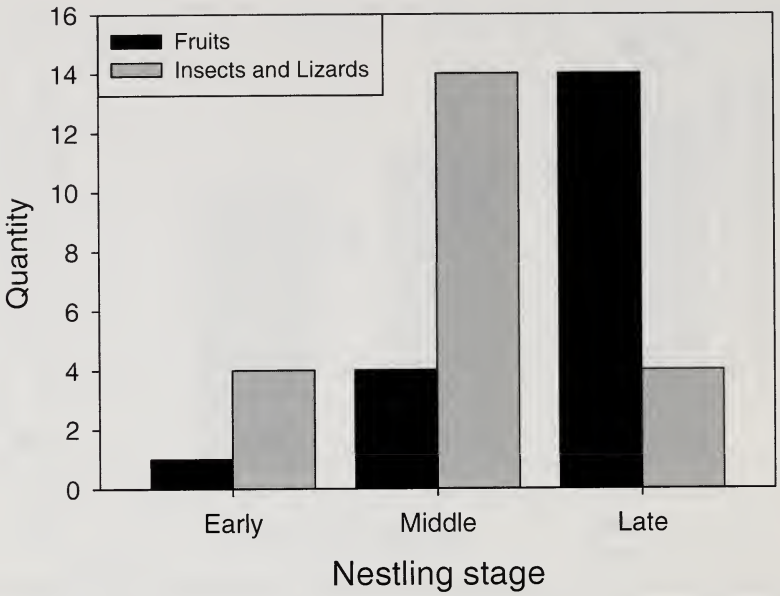


FIG. 3. Foods provided to Red-ruffed Fruitcrow nestlings during early (day 0–16), middle (day 17–22), and late (day 23–35) stages of the nestling period. Two nests were sampled in each period.

bohydrates for other energetic needs, despite adults being almost solely frugivorous. Extremely low provisioning rates may prolong the nestling period but may also reduce risk of nest predation (Skutch 1949). Development rate of nestlings may represent a compromise among energy delivery, physiological tradeoffs, and predation risk.

The Red-ruffed Fruitcrow is a rare neotropical endemic and it is essential that its ecological requirements and reproductive biology be better understood. Further study into the life history and habitat requirements of the Red-ruffed Fruitcrow is clearly needed.

ACKNOWLEDGMENTS

We acknowledge the Venezuela field crews that aided in data collection. Specifically we thank Brian Schwartz, Elena Arriero, Karie Decker, Bruce Robertson, Sophie Walker, and the two anonymous reviewers for helping with manuscript review. This study was made possible by support under NSF grants DEB-9981527 and DEB-0543178 to T. E. Martin. Permit numbers are DM/0000237 from FONACIT, PA-INP-005-2004 from INPARQUES, and 01-03-03-1147 from Ministerio del Ambiente.

LITERATURE CITED

Beehler, B. M. 1986. Birds of Paradise and mating system theory, predictions and observations. Emu 87:78–89.

Breitwisch, R., P. G. Merritt, and G. H. Whitesides. 1984. Why do Northern Mockingbirds feed fruit to their nestlings? Condor 86:281–287.

Briskie, J. V. and S. G. Sealy. 1990. Evolution of short incubation periods in the parasitic cowbirds, *Molothrus* spp. Auk 107:789–793.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. Proceedings of the Royal Society of London, Series B 273:1375–1383.

Ghalambor, C. K. and T. E. Martin. 2001. Fecundity survival trade-offs and parental risk taking in birds. Science 292:494–497.

Hensler, G. L. and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42–53.

Hilty, S. L. 2003. Birds of Venezuela. Second Edition. Princeton University Press, Princeton, New Jersey, USA.

Martin, T. E. 2002. A new view of avian life history evolution tested on an incubation paradox. Proceedings of the Royal Society of London, Series B 269:309–316.

Morton, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. American Naturalist 107(953):8–22.

Pizo, M. A., W. R. Silva, M. Galetti, and R. Laps. 2002. Frugivory in Cotingas of the Atlantic Forest of southeast Brazil. Ararajuba 10:177–185.

Serrano, D. 1994. Seleccion de Habitat, Ciclo Reproductivo y Sistema Lek de Apareamiento de *Pyroderus scutatus*. Thesis. Universidad de Valle, Cali, Colombia.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.
Snow, D. W. 1976. The web of adaptation. Quadrangle Press, New York, USA.
Snow, D. W. 1982. The cotingas: bellbirds, umbrella birds and other species. Comstock Press, Ithaca, New York, USA.
Snow, D. W. 2004. Family Cotingidae (cotingas). Pages 578–579 *in* Handbook of the birds of the world. Volume 9. Cotingas to pipits and wagtails (J. del Hoyo, A. Elliot, and D. Christie, Editors). Lynx Editions, Barcelona, Spain.
Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

The Wilson Journal of Ornithology 120(4):867–871, 2008

Nests and Nesting Behavior of Golden Swallow (*Tachycineta euchrysea*) in Abandoned Bauxite Mines in the Dominican Republic

Jason M. Townsend,[1,4] Esteban Garrido,[2] and Danilo A. Mejia[3]

ABSTRACT.—Little information is available on nesting of Golden Swallow (*Tachycineta euchrysea*), a threatened species that occurs only on the island of Hispaniola. We report on six nests discovered and monitored in abandoned bauxite mines in the Sierra de Bahoruco of the Dominican Republic. Nests were in cavities of the vertical walls of these pit mines. Clutch sizes consisted of 2–4 eggs and the nestling stage lasted between 21 and 24 days with both parents provisioning the brood. Three of the six nests were depredated by introduced mammals. We compare our observations of Golden Swallow nesting success to nesting studies of congeneric swallows and emphasize the potential conservation importance of a nest box placement and monitoring program on Hispaniola. *Received 3 January 2008. Accepted 6 May 2008.*

The Golden Swallow (*Tachycineta euchrysea*) is a rare and poorly described species that occurs only on Hispaniola, the Greater Antillean island politically divided between Dominican Republic and Haiti. Historically, the range of Golden Swallow also included Jamaica, but it has not been reported there since 1989 and causes of this local extirpation are unknown (Raffaelle et al. 1998). On Hispaniola, where populations have declined over the last 30 years, the species is increasingly restricted to isolated remnant patches of montane forest from 750 m elevation to the highest forested peaks (Birdlife International 2000, Keith et al. 2003, Latta et al. 2006). Golden Swallows appear to prefer Hispaniolan pine (*Pinus occidentalis*) and mixed pine-broadleaf forests, but occasionally forage over open agricultural areas and natural savannahs (JMT, pers. obs.). The species occurs in the Massif de la Hotte of Haiti, Sierra de Bahoruco/Massif de la Selle along the border between the two nations, and in Sierra de Neiba and Cordillera Central of the Dominican Republic (Keith et al. 2003).

The Golden Swallow is a cavity-nesting species, reported to occasionally nest in colonies (Dod 1992), but detailed descriptions of its nesting ecology are lacking. The species has been observed in the Cordillera Central nesting in cavities of *Cecropia schreberiana* with 12 nests reported in one stand of four trees during May 1975 (Dod 1992). Multiple adults were observed delivering insects to these nests but the author did not report cavity size, number of nestlings, or structure of the nest. Individuals in the Sierra de Bahoruco have been observed constructing nests in cavities of living and dead emergent snags of *Didymopanax tremulus*, at heights estimated to be 14–16 m (JMT, pers. obs.). Similar observations of individuals investigating cavities in emergent hardwoods and hardwood snags

[1] Department of Environmental and Forest Biology, State University of New York, College of Environmental Science and Forestry, Syracuse, NY 13210, USA.
[2] Grupo Jaragua, Calle El Vergel 36, Ensanche El Vergel, Santo Domingo, Dominican Republic.
[3] Sociedad Ornitológica de la Hispaniola, Galerías Comerciales Suite 202, Avenida 27 de Febrero 54, Santo Domingo, Dominican Republic.
[4] Corresponding author; e-mail: jatownse@syr.edu

TABLE 1. Golden Swallow nest and nest-site characteristics in abandoned bauxite mines, Sierra de Bahoruco, Dominican Republic, 2004.

Characteristic	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5	Nest 6	Mean ± SD
Cavity substrate	soil/rock	soil/rock	soil	rock	soil/rock	rock	
Height above ground (m)	2	2.7	0.3	3.5	5	5	3.1 ± 1.8
Depth of cavity (cm)	16	18	28.5		23.6		21.5 ± 5.7
Width of cavity (cm)	9	9.8	11.9		9.2		10.0 ± 1.3
Height of cavity (cm)	8	9.9	5.2		5.8		7.2 ± 2.2
Width of entrance (cm)	4	5.7	7.7		9.2		6.7 ± 2.3
Height of entrance (cm)	3	2.6	5.2		5.8		4.2 ± 1.6
Elevation (m)	1,092	1,424	1,306	1,306	1,424	1,395	1,325 ± 126
Direction of exposure (°)	340	80	210	32	254	172	181 ± 113

have been made in the Sierra de Neiba and Massif de la Hotte (Rimmer et al. 2004, 2005). These cavities are often originally excavated by the endemic Hispaniolan Woodpecker (*Melanerpes striatus*) (Bond 1943). Additionally, there are reports of nesting in snags of Hispaniolan pine, especially in recently burned stands (E. M. Fernandez, pers. comm.); in caves (Fernandez and Keith 2003); and under the eaves of houses (Bond 1943).

We report six nests of Golden Swallows found in 2004 while conducting field work on other resident species. These nests occurred in abandoned bauxite pit mines surrounded by pine forest between 1,000 and 1,425 m in the Sierra de Bahoruco (18° 07′ N, 71° 33′ W). Pits were generally rounded with a diameter of ~200–500 m and vertical walls that extended 5–35 m below the natural surface of the land. Some forest regeneration is occurring in and around these pits with scattered Hispaniolan pines ranging from 2 to 5 m height and up to 15 cm diameter at breast height. The mines were created with heavy machinery between 1952 and 1982, and were abandoned in 1985. There are multiple earthen depressions and rock-pile crevices along the walls of these pits that provide cavity spaces for nest construction.

OBSERVATIONS

Overall Phenology.—Observations of Golden Swallow nesting activity occurred between early February and 25 July 2004. Pairs of swallows were observed investigating cavities in pit mines and in snags in early February. Nest construction was observed in pit mines on 5 May (entering with pine needles) and in cavities of emergent hardwood species on 10 May (entering with pine needles) and on 16 May (entering with moss). Between 8 May and 25 July we discovered and monitored six active Golden Swallow nests in pit mine habitat. One of the observed nests was depredated on 9 May and an embryo recovered from an intact egg was estimated to be 2–4 days old. Ranges of hatch dates calculated for three of these nests were 25–27 May, 30–31 May and 3 June. Hatch dates for the remaining two nests were estimated to be within 15–30 June and 20–28 June. It is not known if these later nests were re-nests or if Golden Swallows nest asynchronously. Fledging dates for the three successful nests were 17 June, 19 July, and 22 July.

Physical Placement of Nests.—The observed nests were constructed deep within the mining pits and occurred within 5 m of the floor of the pits (Table 1). Nests were constructed in cavities along the vertical walls where rocks had tumbled and formed layers of crevices and openings. The inner walls and ceilings of cavities consisted of limestone boulders while the floors of the cavities were platforms of soil and rock. The soil in this area is a red, bauxite-rich clay with a dry, fine layer at the surface, and all incubating individuals had red-stained ventral body feathers from contact with this soil.

Four of the six nest cavities were accessible for interior measurement and had mean height of 7.2 cm, mean width of 10.0 cm, and mean depth of 21.5 cm (Table 1). Two of the four nest cavities had openings narrower than the interior cavity height with small triangular entrance holes measuring 4.0–5.7 cm at the base and 1.0–2.0 cm at the apex of the triangular openings.

TABLE 2. Incubation and provisioning observations at Golden Swallow nests in abandoned bauxite mines, Sierra de Bahoruco, Dominican Republic, 2004.

	Incubation		Feeding	
Nest #	# min incubating/ # min observed	Mean ± SD duration of incubation period (min)	# min observed	Mean ± SD # provisionings/hr
1	82/136	11.3 ± 3.9	[b]	
2	234/426	5.6 ± 3.3	[c]	
3	167/397	7.6 ± 3.0	221[d]	11.4 ± 1.5
4	[a]		91[e]	11.9
5	[a]		390[f]	12.5 ± 4.2
6	74/120	8.2 ± 3.1	[c]	

[a] Discovered post-hatching.
[b] Depredated during incubation stage.
[c] No data collected during provisioning.
[d] Data collected over 4 days between nestling days 2 and 10.
[e] Data collected on 1 day = nestling day 6.
[f] Data collected over 5 days between nestling days 8 and 16.

Nest Materials.—One of the six nests observed was removed and collected intact after a depredation event. This nest was ovular in shape to accommodate the shape of the cavity and measured 15 × 10 cm. The long end of the oval nest was from the front to the back of the nest cavity. Nest structure consisted primarily of dry pine needles from Hispaniolan pines. These needles were interlaid to form the structural body of the nest and also to level any low points in the earthen floor of the cavity. The inner lining of the nest cup was a tightly woven amalgam of dry hanging moss (40–45% of total material), cotton-like plant material (40–45%), body feathers ranging from 1 to 4 cm in length and oriented with quills buried in the plant material (~5%), woven pine needles (~5%), and flakes of bark (<1%). Golden Swallows were frequently observed aerially collecting moss from hanging branches of Hispaniolan pines. One solitary individual was observed repeatedly feather-dropping outside of a nest cavity before entering the cavity and apparently depositing the feather.

Eggs and Clutch Size.—Clutch size was two to four eggs (2 eggs: $n = 2$; 3 eggs: $n = 2$; 4 eggs: $n = 1$; at least 2 eggs [observed after depredation]: $n = 1$). The natural color of eggs was difficult to ascertain because all those observed appeared to have been stained with the same red soil that stained the body feathers of the incubating adult. Natural egg color appeared to be white to creamy-white with minimal spotting. One egg, recovered intact from a depredated nest, was 18.8 mm in length × 12.8 mm in width at its widest point, smaller than the mean egg size reported for a Caribbean congener, Bahama Swallow (*Tachycineta cyaneoviridis*) (19.4 mm length × 13.9 mm width) (Allen 1996).

Parental Behavior.—Nest observations took place on clear, rain-free days between 0900 and 1500 hrs at a distance from the nest of at least 100 m. All observations were by JMT from a position considered to be hidden from view of the birds where he remained stationary for the duration of the observation (mean duration of observation periods = 76 min, range = 32 – 136 min).

Nesting pairs were dispersed throughout mine habitat and there was no evidence of overlapping territories, communal breeding or coloniality. Four of the six nests were observed during the incubation period (Table 2). Apparently, only one member of the pair incubates, based upon observations of the red, soil-stained ventral body feathers of the entering and exiting individual, and the clean, white body feathers of the other individual observed in the area, but not in the nest cavity. The individual with clean, white body feathers frequently circled within 20 m of the nest cavity vocalizing loudly in the minutes before the red-stained individual exited the cavity, and then foraged with the red-stained individual. Incubating individuals spent 52% of their observed activity on the nest.

Provisioning of young was observed at three of the six nests (Table 2). Both members of the pair provisioned nestlings and were observed removing fecal sacks. We could not as-

certain if brooding behavior was shared between the male and female because the feathers of both pair members became soil-stained during the nestling period. The mean provisioning rate at the three observed nests, each with two nestlings, was 11.9/hr (SD = 0.6).

Time to Fledging and Nesting Success.— Three of the six monitored nests successfully fledged young and three were depredated. The three successful nests hatched and fledged different numbers of young: one fledgling from four eggs, two fledglings from two eggs, and three fledglings from three eggs. Young fledged at 21–24 days of age at two of the three successful nests, based on known hatch dates, within a range of 1 to 3 days; at the third nest, hatch date was only known within a range of 15 days. The three unsuccessful nests were found with disturbed nest cups and the near-complete feather sets of an adult Golden Swallow strewn within and immediately around the cavity area. We assume the incubating or brooding individual was killed during each depredation event.

DISCUSSION

The rate of nest depredation (50%) was higher than reported for other congeners. Depredation was reported for two of eight nests (25%) of Mangrove Swallows (*Tachycineta albilinea*) in Panama (Dyrcz 1984) but was not reported as a cause of failure in 10 nests of Bahama Swallows in Grand Bahama (Allen 1996) nor in 128 nests of White-rumped Swallows (*T. leucorrhoa*) in Argentina (Massoni et al. 2007). Nesting success for 3,458 nests of Tree Swallows (*T. bicolor*) in 10 eastern North American populations was 78.8% and nest predation was not reported as a significant cause of failure (Robertson et al. 1992). Both White-rumped and Tree swallows make extensive use of nest boxes which may be considered less vulnerable to predators than natural cavities.

Potential mammalian nest predators on Hispaniola include Black rats (*Rattus rattus*), Norway rats (*R. norvegicus*), feral cats (*Felis catus*), and Indian mongoose (*Herpestes javanicus*), all invasive species that have been introduced within the last 500 years. An Indian mongoose was observed entering the nest cavity at one Golden Swallow nest within 12 hrs of nest predation, apparently in an attempt to extract the remaining egg in the far depths of the cavity (Townsend 2006). The Indian mongoose is known to be expanding in population on Hispaniola (Horst et al. 2001), and is capable of easily accessing the narrow cavities chosen by Golden Swallows. Placement of nests on or near the ground in open pit mine areas may leave Golden Swallows especially vulnerable to predation by mammalian predators. It is unknown if Golden Swallows nesting in cavities of snags are exposed to high rates of predation, but rats on Hispaniola are known to be highly arboreal and have depredated nests of other resident cavity nesting species (JMT, pers. obs.). Future detailed and more extensive studies should focus on the breeding biology of Golden Swallows in all available habitats to examine nest predation and to place this species' breeding biology in the broader ecological context of a genus that spans much of the Americas.

That Golden Swallows are nesting in mines abandoned within the last 25 years attests to the species' willingness to explore novel habitats. A network of well-placed nest boxes with proper predator protection could be a key component to this species' continued existence. Mangrove, Bahama, and White-rumped swallows have all recently been observed nesting in artificial nest boxes and gourds (Dyrcz 1984, Allen 1996, Massoni et al. 2007). However, nest boxes randomly placed in pine forest and mixed pine-broadleaf habitats of Hispaniola have not been occupied (JMT, pers. obs.). A more focused nest-box placement effort, possibly concentrating on the open mining areas, may result in greater success. A general program of nest box construction, focused nest box placement, intensive monitoring, and predator control could provide a wealth of data on this declining species. The proposed program could also be the basis for potential reintroduction of Golden Swallows into appropriate habitat in Jamaica.

ACKNOWLEDGMENTS

We are grateful for funding support from C. C. Rimmer and the Vermont Center for Ecostudies. We thank V. M. Mejia, M. M. Paulino, and A. K. Townsend for assistance in the field and D. W. Winkler for helpful advice. The manuscript was greatly improved by the constructive comments of D. J. Cerasale and L. J. Woolaver. Logistical support and permission to conduct research in the Dominican Republic was gener-

ously provided by the Subsecretaria de Áreas Protegidas y Biodiversidad and Fundación Moscoso Puello.

LITERATURE CITED

ALLEN, P. E. 1996. Breeding biology and natural history of the Bahama Swallow. Wilson Bulletin 108: 480–495.

BIRDLIFE INTERNATIONAL. 2000. Threatened birds of the world. Lynx Editions and BirdLife International, Barcelona, Spain and Cambridge, United Kingdom.

BOND, J. 1943. Nidification of the passerine birds of Hispaniola. Wilson Bulletin 55:115–125.

DOD, A. S. 1992. Endangered and endemic birds of the Dominican Republic. Cypress House Press, Fort Bragg, California, USA.

DYRCZ, A. 1984. Breeding biology of the Mangrove Swallow and the Gray-breasted Martin at Barro Colorado Island, Panama. Ibis 126:59–66.

FERNANDEZ, E. M. AND A. R. KEITH. 2003. Three unusual bird nests from the Dominican Republic. Journal of Caribbean Ornithology 16:73–74.

HORST, G. R., D. B. HOAGLAND, AND C. W. KILPATRICK. 2001. The mongoose in the West Indies: the biogeography and population biology of an introduced species. Pages 409–424 *in* Biogeography of the West Indies: patterns and perspectives (C. A. Woods and F. E. Sergile, Editors). CRC Press, Boca Raton, Florida, USA.

KEITH, A. R., J. W. WILEY, S. C. LATTA, AND J. A. OTTENWALDER. 2003. The birds of Hispaniola: Haiti and the Dominican Republic. An annotated checklist. British Ornithologists' Union and British Ornithologists' Club, Tring, Herts, United Kingdom.

LATTA, S., C. RIMMER, A. KEITH, J. WILEY, H. RAFFAELE, K. MCFARLAND, AND E. FERNANDEZ. 2006. Birds of the Dominican Republic and Haiti. Princeton University Press, Princeton, New Jersey, USA.

MASSONI, V., F. BULIT, AND J. C. REBOREDA. 2007. Breeding biology of the White-rumped Swallow in Buenos Aires Province, Argentina. Ibis 148: 10–17.

RAFFAELE, H. A., J. W. WILEY, O. H. GARRIDO, A. R. KEITH, AND J. RAFFAELE. 1998. A guide to the birds of the West Indies. Princeton University Press, Princeton, New Jersey, USA.

RIMMER, C. C., J. ALMONTHE, E. GARRIDO, D. A. MEJIA, M. MILAGROS, AND P. R. WIECZORECK. 2004. Bird records in a montane forest fragment of western Sierra de Neiba, Dominican Republic. Journal of Caribbean Ornithology 16:55–60.

RIMMER, C. C., J. M. TOWNSEND, A. K. TOWNSEND, E. M. FERNANDEZ, AND J. ALMONTE. 2005. Avian diversity, abundance, and conservation status in the Macaya Biosphere Reserve of Haiti. Ornitología Neotropical 16:219–230.

ROBERTSON, R. J., B. J. STUTCHBURY, AND R. R. COHEN. 1992. Tree Swallow (*Tachycineta bicolor*). The birds of North America. Number 11.

TOWNSEND, J. M. 2006. Predation of a Golden Swallow nest by the Indian mongoose in the Sierra de Bahorucos, Dominican Republic. Journal of Caribbean Ornithology 19:108–109.

The Wilson Journal of Ornithology 120(4):871–874, 2008

Nest, Nestling Care, and Breeding Season of the Spangled Cotinga (*Cotinga cayana*) in French Guiana

Johan Ingels[1]

ABSTRACT.—I report a nest, nestling care, and the breeding season of the Spangled Cotinga (*Cotinga cayana*) near Saül, French Guiana. The open cup nest was found on 20 October 2007 with a 15–20 days old nestling, ~12 m above ground in a yellow mombin tree (*Spondias mombin*). Nest activities were followed during 4 days, from dawn to dark. The nestling's plumage had a scaled color pattern like that of the female, but was paler gray. The female left the nest between 0600 and 0630 hrs in the morning, and provisioned the nestling 6–8 times a day. Food items delivered to the nestling were mainly bluish to blackish fruits, ~6–7 mm in diameter, but also included a ~6 cm cricket (Orthoptera) and a ~10 cm lizard. The female arrived for a last provisioning between 1630 and 1710 hrs, after which she stayed with the nestling until morning. This and other records of breeding Spangled Cotingas suggest that nesting coincides with the dry season. *Received 24 January 2008. Accepted 26 May 2008.*

The seven species of blue cotingas in the genus *Cotinga* form a distinct group within the Cotingidae; little is known about their diet, foraging behavior, vocalizations, displays, reproduction, and timing of breeding (Snow

[1] Galgenberglaan 9, B-9070 Destelbergen, Belgium; e-mail: johan.ingels@skynet.be

1982, 2004; Brooks et al. 1999; Chaves 2001; Sánchez et al. 2007). *Cotinga* species have wide gapes and consume figs, mistletoe berries, palm and lauraceous fruits, and have also been recorded taking animal prey, including flying termites and ants, and small amphibians (Snow 1982, 2004). The Spangled Cotinga (*Cotinga cayana*) is the most widespread *Cotinga* species, occurring throughout the Amazon Basin and Guianan shield (Snow 2004). Three Spangled Cotinga nests have been reported: a nest containing one egg on 21 August 1924 near Belém, Brazil (Pinto 1953); a female with a nestling collected on 24 February 1946 near Villavicencio, in the eastern Andes of Colombia (Nicéforo 1947); and a female constructing a nest on 2 October in the Réserve Naturelle Les Nouragues in French Guiana (Tostain et al. 1992). I describe a nest of a Spangled Cotinga in French Guiana, report on the behavior of the female and nestling at the nest, describe food items brought to the nestling, and discuss timing of the breeding season.

OBSERVATIONS

I observed a single Spangled Cotinga nest between 20 and 23 October 2007 at Saül (3° 37′ N, 53° 12′ W, ~200 m ASL) in the interior of French Guiana. This small village of ~70 inhabitants occupies a clearing of ~75 ha surrounded by primary lowland forest. The ~1–ha garden on the village outskirts where the nest was found had cottages for ecotourists with continuous forest on two sides and adjacent gardens on the other. It was planted with flowering shrubs (e.g., *Hibiscus* and *Poinciana* spp.) and fruiting trees (e.g., *Cocos nucifera*, *Mangifera indica*, *Persea americana*, *Musa* spp., and *Citrus* spp.). Human impact on the forest around the village is restricted to an airstrip, selective logging for local construction needs, and a few isolated inhabited clearings and agricultural lands, scattered away from the village. Events at the nest were observed from a distance of ~20 m with 7 × 35 binoculars. I recorded the behavior of the female caring for the nestling, food items brought to the nestling, and nestling behavior from dawn to dark during 4 days.

On the morning of 20 October 2007, a female Spangled Cotinga with a ~6 cm cricket (Orthoptera) in her bill was perched on top of a ~15 m dead tree at the edge between forest and garden. Minutes later, I observed the female perching on a ~25 cm thick branch, inside the crown of a yellow mombin tree (*Spondias mombin*, Anacardiaceae), ~25 m from the dead tree. After sitting there motionless for several minutes, she hopped slowly down the branch to arrive at a nest, where she fed the cricket to a nestling. I estimated the nestling to be 15–20 days of age based on a presumed nestling period of ~30 days for *Cotinga* species (Snow 1982). The nestling had pin feathers over its entire body, half grown remiges, and a ~25 mm long tail. A few tufts of grayish down still adhered to the head feathers. The nestling's plumage had a scaled color pattern like that of the female, but was paler gray. It was characterized by grayish tips on primaries, secondaries, greater wing-coverts, and rectrices. The outer edges of the secondaries were also grayish. The dorsal feathers had broader pale grayish edges and the ventral plumage was paler than in the adult female.

The nest tree was ~18 m tall and isolated in the garden among a few low fruiting trees, mostly *Citrus* spp. The nest site was the flatter part of a crotch at a height of ~12 m between two branches with a diameter of ~25 cm, not surrounded by foliage, and was illuminated and visible from all sides. The nest was a tiny cup with an outer diameter of ~5 cm and a height of ~1.5 cm, finished with grayish lichens or a grayish-white fungal mycelium on the outside. The overall grayish appearance of nest and nestling blended well with the grayish bark of the yellow mombin tree.

The nestling was fed and cared for by the female only. I previously observed a male near the nest site on 6 October 2007, but did not see a male near or at the nest, nor any interaction between the female and a male. The female left the nest between 0600 and 0630 hrs in the mornings of 21–23 October to return with food 25, 40, and 15 min later, respectively. Normally, the female arrived with a dark bluish to blackish berry in her bill, 6–7 mm in diameter, which she fed to the nestling, followed by 5–7 more berries by regurgitation. On 23 October 2007, the female arrived at the nest at 1710 hrs with a ~10 cm long lizard in her bill, which she presented head first to the nestling and which it managed

to swallow. Mean (± SD) intervals between feedings during the day were 107 ± 12 min (n = 12) and ranged between 85 and 120 min for a total of 6–8 feedings a day. All provisioning of the young was done in silence. The female did not fly directly to the nest when arriving with food, often first perching in the dead tree for several minutes, before flying to the yellow mombin tree. Once in this tree, it took another 5–10 min to approach the nest. Normally she arrived at the nest by hopping down in ~0.5 m intervals along one of the thick branches of the fork. To be fed, the nestling raised its head and opened its bill without any begging calls. Minutes after being fed, the nestling turned its posterior up to the female, producing one, rarely two fecal sacs, which the female swallowed. Each feeding session was followed by the female brooding the nestling for 25–80 min (mean ± SD = 51 ± 21 min, n = 7). The female arrived in the evening at the nest for a last feeding between 1630 and 1710 hrs (mean ± SD = 1653 hrs ± 17 min, n = 3). After the last feeding, the female stayed with the nestling until morning.

During daytime brooding sessions, the nestling usually sat in front of the female, occasionally partly covered by her breast feathers. In bright sun, the female spread her wings slightly shading the nestling. During brooding sessions, as well as during periods when the female was away from the nest, the nestling alternated long bouts of prone roosting upon the nest with short bouts of feather preening and wing exercising. When the nestling was on its own in the nest and in full sunlight, it stretched its head upward with bill wide open and spread its wings slightly, perhaps in an effort to thermoregulate. At night, the nestling was entirely covered by the female.

DISCUSSION

The nest described is only the fourth reported for the Spangled Cotinga (Nicéforo 1947, Pinto 1953, Tostain et al. 1992). The nest was a tiny structure for a cotinga with a length of 20 cm and a mean mass of ~65 g (Snow 1982). The gray material on the outside of the nest and the gray color pattern of the nestling made both inconspicuous against the gray bark of the nest tree. My observations of an apparent single egg clutch size, and camouflaged nest and nestling were consistent with those of others (Nicéforo 1947, Pinto 1953).

Movements of the female near the nest were reduced to a minimum. When approaching the nest, she often stopped, perching motionless for minutes before finally arriving at the nest. The nestling begged for food by simply raising its head and gaping. At the nest, the female and nestling Spangled Cotinga were silent. It is evident the nest, nestling, and behavior of both female and nestling are all highly adapted to avoid predation (Snow 2004).

Snow (2004) estimated nest construction to last ~20 days, an incubation period of ~20 days, and a nestling period of ~30 days for *Cotinga* species. Assuming this is accurate, construction of the nest I found would have started at the end of August, a single egg would have been laid in the first half of September and the nestling would fledge at the beginning of November if it survived. Tostain et al. (1992) observed a female building a nest on 2 October. The breeding season of the Spangled Cotinga in French Guiana appears to coincide with the drier period of the year from the end of July until the end of November. Nesting records in Brazil and Colombia also occurred during local dry seasons (Nicéforo 1947, Pinto 1953).

ACKNOWLEDGMENTS

I thank Frederik Brammer, Daniel M. Brooks, Pierre-Yves Henry and César Sánchez M. for help with relevant literature, Scott Mori for identifying the nest tree, Olivier Claessens for information about the abundance of *Cotinga* species in French Guiana, and Des Jackson and two anonymous referees for helpful comments on the manuscript. I am grateful to Lucien Timane for allowing me to work freely on his property.

LITERATURE CITED

Brooks, D. M., L. Pando-Vasquez, and A. Ocmin-Petit. 1999. Comparative life history of cotingas in the northern Peruvian Amazon. Ornitología Neotropical 10:193–206.

Chaves, L. 2001. Observations on diet, foraging behaviour, vocalisations and displays of Spangled Cotinga *Cotinga cayana*. Cotinga 16:103–104.

Nicéforo, M. H. 1947. Notas sobre aves de Colombia II. Caldasia 4:317–377.

Pinto, O. M. de O. 1953. Sobre a coleção Carlos Estevão de pelos, ninhos e ovos das aves de Belém (Pará). Papéis Avulsos do Departamento de Zoologia São Paulo 11:111–222.

Sánchez, C., V. Ruiz-Gutiérrez, and D. Martínez. 2007. Description of male vocalizations of the Turquoise Cotinga (*Cotinga ridgwayi*). Wilson Journal of Ornithology 119:455–458.

Snow, D. 1982. The cotingas. Cornell University Press, Ithaca, New York, USA.

Snow, D. 2004. Family Cotingidae (cotingas). Pages 32–108 *in* Handbook of the birds of the world. Volume 9. Cotingas to pipits and wagtails (J. del Hoyo, A. Elliott, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Tostain, O., J.-L. Dujardin, C. Érard, and J.-M. Thiollay. 1992. Oiseaux de Guyane (The birds of French Guiana). Société d'Études Ornithologiques, Brunoy, France.

The Wilson Journal of Ornithology 120(4):874–878, 2008

Nests, Eggs, and Incubation Behavior of Grey-headed Bullfinch (*Pyrrhula erythaca*)

Jia Chenxi[1,2] and Sun Yuehua[1]

ABSTRACT.—We describe characteristics of nest sites, nests, and the first report of the eggs and incubation behavior of the Grey-headed Bullfinch (*Pyrrhula erythaca*). We found nine nests in coniferous forest during June and July 2003 at Lianhuashan Natural Reserve in central China. Only the female built the nest, but her mate remained in close attendance. Nests were cup shaped and built on horizontal branches of coniferous trees, 1.3–16.0 m above ground. Clutch size was three eggs ($n = 3$); the eggs were white in color and spotted with reddish brown. Only the female incubated and averaged 85% nest attendance. On-nest and off-nest bouts ($\bar{x} \pm$ SD) were 31 ± 17 min and 4 ± 5 min, respectively. Egg color, egg size, and clutch size were similar to those reported for other bullfinches, but nest materials differed slightly. *Received 24 September 2007. Accepted 30 January 2008.*

The genus *Pyrrhula* consists of six species of bud-eating birds of which five species occur in China. Bullfinches have a Palearctic distribution, including the Azores and Japan. The breeding biology of the Eurasian Bullfinch (*P. pyrrhula*), which has the widest distribution, has been well studied, but relatively little is known of the other species. The Grey-headed Bullfinch (*P. erythaca*) is distributed in the Himalayan Mountains, central China, and Taiwan, and breeds in mixed coniferous and deciduous forests (Cheng 1987). The natural history of the Grey-headed Bullfinch is poorly documented and little is known about its breeding. We previously published a note on the nestlings and nestling behavior of this species based on observation of one nest (Jia et al. 2003). Ali and Ripley (1996: 210) described one nest as "the usual frail bullfinch type about twelve feet (3.6 m) from the ground on top of a young pine tree. It contained young birds about a week old on 19 July". There are no published descriptions of the eggs of this species. The objective of this paper is to provide descriptions of the nest, eggs, and incubation behavior of the Grey-headed Bullfinch.

METHODS

Study Area.—This study was conducted in the Lianhuashan Natural Reserve in Gansu Province, central China (34° 40′ 67″ N, 103° 30′ 84″ E). Forest habitat occurs in the reserve on north-facing slopes, and some northeast and northwest-facing slopes between 2,600 and 3,600 m. Only shrubs and grasses grow on south-facing slopes. The main cover types in our study area are: (1) coniferous forest dominated by fir (*Abies fargesii*) and spruce (*Picea asperata*); (2) coniferous-deciduous forest including spruce, fir, birch (*Betula utilis*), and willows (*Salix* spp.); and (3) shrublands including willows, sea buckthorn (*Hippophae rhamnoides*), and grasses. Mean annual temperatures range from 5.1 to 6.0° C with a maximum of 34.0° C and minimum of −27.1° C. The climate is semiarid and, in the

[1] Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China.

[2] Corresponding author; e-mail: jiacx@ioz.ac.cn

TABLE 1. Grey-headed Bullfinch nests observed in the Lianhuashan Natural Reserve, Gansu Province, central China during June and July 2003.

		Nest tree		Nest			
Nest	Date found	Species	DBH (cm)	Stage	Height above ground (m)	Distance to the trunk (m)	Fate
1	17 Jun	Fir	36	Nest-building	4.2	5	Abandoned
2	18 Jun	Fir	24	Incubation	9.0	1.4	Successful
3	20 Jun	Spruce	—	Nest-building	8.0	—	Abandoned
4	28 Jun	Fir	34	Incubation	1.3	2.2	Abandoned
5	1 Jul	Spruce	22	Incubation	16.0	0.8	Successful
6	2 Jul	Spruce	34	Nest-building	7.0	3	Successful
7	3 Jul	Spruce	34	Egg-laying	2.8	2.4	Abandoned
8	3 Jul	Fir	28	Nestling	2.2	2.4	Successful
9	13 Jul	Fir	34	Incubation	7.0	3	Successful

higher elevations, the annual precipitation is ~65 cm. The study area has been described in more detail by Sun et al. (2003).

Field Procedures.—We systematically searched for nests from June to July 2003. Nests were located by visually following females that were either carrying nesting materials or returning to the nest following an incubation break, or by following adults provisioning young with food. We also used the location of males as they called to incubating females. Egg length and breadth were measured to the nearest 0.02 mm with vernier calipers, while egg mass was weighed to the nearest 0.1 g using an electronic scale. All measurements were obtained during incubation recesses.

Incubation behaviors of females were observed at two nests. We monitored one nest 7 m above ground using a digital video camcorder at a distance of 10 m. We videotaped the nest five times for 1 to 3 hrs each time on 13 and 14 July. The second nest was 1.3 m above ground and was continuously monitored for 44 hrs and 21 min through use of a Gemini Temperature Data Logger (Gemini Data Loggers UK Ltd, Chichester, UK) from 1639 hrs (Beijing time) on 29 June to 1300 hrs on 1 July when the nest was abandoned. The data logger probe was inserted into a dummy egg that contained paraffin wax and arranged among the eggs of the nest. Temperature of the dummy egg was recorded by the data logger and indicated when the incubating female was on or off nest. We also visually observed the nest after installing the data logger for 102 min on 29 June to verify the validity of this method. All observers were in camouflage and all video equipment was camouflaged using branches and leaves.

We measured canopy cover, shrub cover, and ground cover on 10 × 10 m square plots at each nest to describe the nest microhabitat. Nests and microhabitat measurements were taken after nests were completed or abandoned. All data are presented as means ± SD.

RESULTS

Nine nests were found in the spruce-fir forest during June and July 2003 (Table 1) at an altitude of ~2,850 m. Three nests were found during early nest-building stages on 17 June, 20 June, and 2 July. Two of these nests were later abandoned. During nest building, the female brought materials to the nest accompanied by the male on five observations at the three nests. We recorded three nest-building visits during one 17-min bout at one nest.

Five nests were found in laying or incubation periods. One female was flushed from a nest on 3 July as we checked whether the nest was active. This nest contained one egg and was abandoned, probably because of our disturbance. Four nests were found from 18 June to 13 July during incubation. One nest was found on 3 July with three nestlings that fledged 2 days later. The male called the incubating female from the nest and provided her with food at a nearby tree during the incubation period.

Nests were on horizontal branches of coniferous trees (Fig. 1) with mean diameter at breast height (DBH) of 31 ± 5 cm (n = 8). Mean height of the nests was 6.2 ± 4.8 m

FIG. 1. Nest site of the Grey-headed Bullfinch.

(range = 1.3–16.0 m, n = 8) above ground level. Mean distances of the nests to the trunk and to the end of the branch were 2.5 ± 1.3 m (range = 0.8–5.0 m) and 0.9 ± 0.4 m (range = 0.4–1.4 m) (n = 8), respectively. Nests were loosely constructed of twigs and lined with fine rootlets. Nests were an open cup shape (Fig. 2); measurements for four nests were 6.5 ± 0.5 cm inside diameter, 13.2 ± 2.3 cm outside diameter, 3.5 ± 0.3 cm inside depth, and 7.5 ± 2.4 cm outside height.

Nest trees were on slopes with a mean slope of 12° (n = 8, range = 2 – 25°). Mean ground cover within 10 × 10 m sampling plots around eight nests was visually estimated to be 85% (70–90%) grass. Mean shrub cover within the plots was 48% (10–80%). Mean canopy cover above the nests was 54% (30–80%) and tree density in the sampling plots around the nests was 3.1 (1–7) trees per 100 m^2 plot.

All complete clutches consisted of three eggs (n = 3). The eggs were pale white with small reddish brown spots, mostly at the large end (Fig. 2). Ten eggs from four nests measured 21.33 ± 0.67 mm long (range = 20.40 –22.24 mm) by 14.86 ± 0.48 mm wide (range = 14.06–15.60 mm), and weighed 2.3 ± 0.2 g (range = 2.0 – 2.7 g).

Thirty-four on-bouts and 35 off-bouts were recorded by the data logger during the period monitored (excluding one abnormal 118 min off-bout and one incomplete 85 min on-bout from all analysis which were the last off-bout and on-bout before the nest was abandoned) (Fig. 3). We recorded activity for one complete diurnal cycle on 30 June from 0610 hrs when the female made an initial departure to 2003 hrs (her last arrival). During this period the female had 25 on/off bouts.

Ten on-bouts and 12 off-bouts were recorded in 567 min at the nest monitored by the video camera. Videos showed the female incubated alone. The mean on-bout duration, combining the nest with the data logger and the nest with the video camera, was 31 ± 17

FIG. 2. Nest and eggs of the Grey-headed Bullfinch.

min (range = 1–73 min), 89% of which were between 10 and 60 min (n = 44 on-bouts). The mean off-bout duration (both monitored nests) was 4 ± 5 min (range = 1–24 min), 77% of which was within 5 min (n = 47 off-bouts). All of six off-bouts of more than 10 min were between 12 and 24 min. The two females had similar nest attentiveness patterns

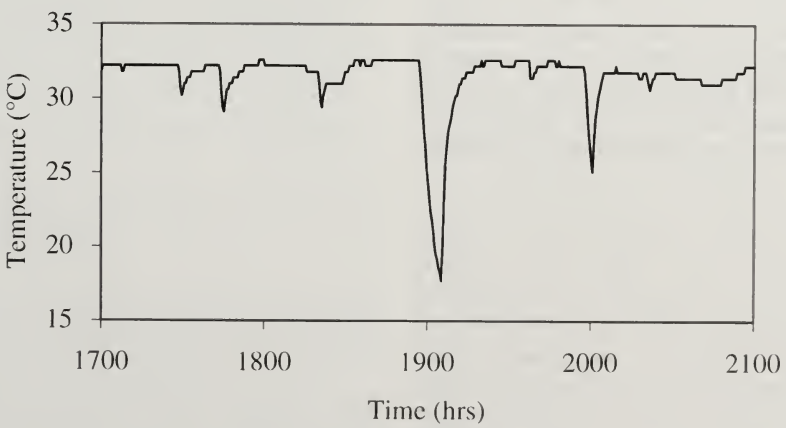


FIG. 3. Egg temperature recordings of the on/off nest differences at one Grey-headed Bullfinch nest during 1700–2100 hrs on 29 June 2003 in Lianhuashan Natural Reserve, Gansu Province, central China. Temperatures were recorded every 30 sec during the incubation period with a Gemini Temperature Data Logger.

(percent total monitored time females were incubating, excluding night, 1,818 min total observed time); the female at the data logger nest incubated 85% of the time while the female at the nest with the video camera incubated 86% of the time (mean for both nests = 85%).

DISCUSSION

Grey-headed Bullfinches appeared to be easily disturbed and prone to abandon their nests during the course of nest construction and egg laying. Three nests were deserted not long after being discovered. One nest desertion in the egg laying period was most likely because of our disturbance; the reasons for the other two cases are unknown as they received little disturbance from researchers during field work.

All observed nests were on branches of larger conifer trees (DBH > 22 cm). This differs from Ali and Ripley (1996)'s description of one nest that was on top of a young pine (*Pinus* spp.) tree. Only the female, accompanied by the male, built the nest during five nest-building attempts observed. The male called the incubating female from the nest to provide her with food at a nearby tree during the incubation period, consistent with observations of the Orange Bullfinch (*P. aurantiaca*) (Roberts 1992).

Nest materials of the Grey-headed Bullfinch differed slightly from those reported in nests of the Red-headed Bullfinch (*P. erythrocephala*), Orange Bullfinch, and Eurasian Bullfinch, which contained moss besides twigs and rootlets, and even a few hairs (Orange Bullfinch) and grass (Eurasian Bullfinch) (Ali and Ripley 1996, Snow and Perrins 1998). Egg color and size were similar to those of the Orange Bullfinch and Red-headed Bullfinch (Ali and Ripley 1996). Our observed clutch size of the Grey-headed Bullfinch was three eggs, similar to that reported for the Orange Bullfinch (3–4 eggs) (Roberts 1992).

The Orange Bullfinch was reported to probably lay two clutches from June to early August (Roberts 1992), and the Eurasian Bullfinch at times laid three clutches from late April to late August (Snow and Perrins 1998). Grey-headed Bullfinch nests were found in a variety of nesting stages in early July with one nest fledging and another in the building stage. This suggests that renesting after a failed nest is possible and, although we have no evidence on double clutches, some birds may be double brooded.

ACKNOWLEDGMENTS

We thank Fang Yun, Zhao Shiqing, Li Jinlin, and staff of the Lianhuashan Natural Reserve for assistance in the field. This study was funded by the National Natural Science Foundation of China (30370204, 30670284, and 30620130110).

LITERATURE CITED

Ali, S. and S. D. Ripley. 1996. Handbook of the birds of India and Pakistan. Second Edition. Volume 10. Oxford University Press, New Delhi, India.

Cheng, Tso-hsin. 1987. A synopsis of the avifauna of China. Science Press, Beijing, China.

Jia, C. X., Zh. Wang, and Y. H. Sun. 2003. A short note on nestling behaviour of Grey-headed Bullfinch at Lianhuashan Natural Reserve, Gansu, China. Sichuan Journal of Zoology 22:17.

Roberts, T. J. 1992. The birds of Pakistan. Volume 2. Oxford University Press, Karachi, Pakistan.

Snow, D. W. and C. M. Perrins. 1998. The birds of the Western Palearctic. Volume 2. Oxford University Press, Oxford, United Kingdom.

Sun, Y. H., J. E. Swenson, Y. Fang, S. Klaus, and W. Scherzinger. 2003. Population ecology of the Chinese Grouse, *Bonasa sewerzowi*, in a fragmented landscape. Biological Conservation 110: 177–184.

The Wilson Journal of Ornithology 120(4):879–883, 2008

Parental Care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) Seedeaters

Carolina Facchinetti,[1] Alejandro G. Di Giacomo,[2] and Juan C. Reboreda[1,3]

ABSTRACT.—The genus *Sporophila* (Emberizidae) comprises species of small finches characterized by marked sexual dichromatism, which in birds is positively associated with extent of female bias in parental care. We analyzed differences in parental care in Tawny-bellied (*S. hypoxantha*) and Rusty-collared (*S. collaris*) seedeaters. We video-recorded nest activity during incubation and when young were 2–4 and 7–9 days of age. Females of both species built the nest and incubated the eggs alone. Female Tawny-bellied Seedeaters: (1) incubated 59% of the time, (2) had a higher frequency of nest visits than males when chicks were 2–4 days of age, and (3) their visits were longer because after feeding they remained in the nest brooding the chicks. There were no gender differences in frequency of nest visits when chicks were 7–9 days of age, but visits of females were longer than those of males. Female Rusty-collared Seedeaters: (1) incubated 51% of the time and (2) had a higher frequency of nest visits when chicks were 7–9 days of age. Both males and females brooded chicks and there were no gender differences in frequency and length of nest visits when chicks were 2–4 days of age. Parental care in both species is female biased, but the extent of male care is slightly higher in Rusty-collared than in Tawny-bellied seedeaters. *Received 4 February 2008. Accepted 29 April 2008.*

The most common mating pattern among birds is social monogamy with biparental care (Lack 1968, Silver et al. 1985, Neudorf 2004). However, there is a considerable variation in type and extent of male care within monogamous species, as males may or may not defend territories, build the nest, incubate the eggs, brood and deliver food to the nestlings, and assist fledglings after they leave the nest (Clutton-Brock 1991).

[1] Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II, Ciudad Universitaria, C1428EGA, Buenos Aires, Argentina.

[2] Departamento de Conservación, Aves Argentinas/Asociación Ornitológica del Plata, Matheu 1246, C1249AAB Buenos Aires, Argentina.

[3] Corresponding author; e-mail: reboreda@ege.fcen.uba.ar.

The genus *Sporophila* (Emberizidae) comprises 31 species of small finches that inhabit grassy open and semi-open habitats from Mexico to central Argentina (Meyer de Schauensee 1952, Ridgely and Tudor 1989). All *Sporophila* species are characterized by a marked plumage-color dimorphism with males strongly patterned and colorful, and females duller and similar between species (Ridgely and Tudor 1989). Variation in melanin-based dichromatism in birds is positively associated with extent of gender bias in passive brood defense (Owens and Hartley 1998). Males of dichromatic species are less likely to participate in nest building (Soler et al. 1998) and to share incubation with females (Verner and Willson 1969).

The reproductive biology of *Sporophila* seedeaters is little studied and most research was in Central America (i.e., Gross 1952, Skutch 1954, Alderton 1961, Stutchbury et al. 1996, but see Marcondes-Machado 1997, Francisco 2006). These studies indicate that most *Sporophila* seedeaters are socially monogamous and have biparental care, but do not report details of sexual differences in parental care.

The reproductive biology of Tawny-bellied Seedeater (*S. hypoxantha*) and Rusty collared Seedeater (*S. collaris*) is virtually unknown, except for the work of Di Giacomo (2005). Tawny-bellied Seedeaters are included within the "capuchinos", a monophyletic group of 11 species (Lijtmaer et al. 2004) that share a similar male plumage coloration pattern (Ridgely and Tudor 1989). Rusty-collared Seedeaters are included in a different clade than Tawny-bellied Seedeaters (Lijtmaer et al. 2004) allowing us to compare gender differences in parental care between species that are relatively distant within the genus. The objectives of our study were to: (1) analyze the extent of gender bias in parental care in *S. hypoxantha* and *S. collaris*, and (2) compare gen-

der differences in parental care between these species.

METHODS

Study Area.—The study was conducted at Reserve El Bagual (26° 10′ S; 58° 56′ W), in the Province of Formosa, Argentina, during breeding seasons 2004–2005 and 2005–2006. This 3,300-ha reserve is in the region of the eastern or humid Chaco. Average annual rainfall in the area is 1,500 mm with mean monthly temperature varying from 16.9° C in July to 26.7° C in January.

Study Species.—Tawny-bellied Seedeaters are sexually dichromatic but genders do not differ in body size (~8–9 g). They are residents at our study site and nest in dry grasslands of *Elionurus muticus* and *Imperata brasiliensis* or *Andropogon lateralis*, and in wet grasslands of *Paspalum intermedium* and *Sorghastrum setosum*. Laying starts during the second half of October and continues until the second half of March. The nest is a deep semispherical open cup built at a height of ~70 cm above ground level. Clutch size is 2–3 eggs; incubation starts with the laying of the penultimate egg and lasts 11–12 days. Young fledge when they are 9–10 days of age (Di Giacomo 2005).

Rusty-collared Seedeaters are sexually dichromatic and males and females do not differ in body size (~12–13 g.). They are residents at our study site and nest in wetlands of *Cyperus giganteus* from early November to early April. The nest is a semispherical open cup built at a height of 1–1.5 m above ground level. Clutch size is 2–3 eggs; incubation starts with laying of the penultimate egg and lasts 12–13 days. Young leave the nest when they are 9–12 days of age (Di Giacomo 2005).

Data Collection.—We searched for nests during the breeding season and visited nests daily or every other day to identify start of laying and date of hatching. We recorded nest-building activity in 18 nests of Tawny-bellied Seedeaters and 10 nests of Rusty-collared Seedeaters. We recorded the gender of the individual that carried nest material during 3–4 consecutive trips for each nest (~15–25 min of observation/nest). We video-recorded nest activity using a Sony Hi8 CCD video camera placed 1.5–2 m from the nest. Video records lasted between 2 and 4 hrs. We video recorded six nests during incubation (12 hrs of video records) for Tawny-bellied Seedeaters, 13 nests with chicks 2–4 days of age (36 hrs), and five nests with chicks 7–9 days of age (12 hrs). We video recorded four nests of Rusty-collared Seedeaters during incubation (8 hrs), four nests with chicks 2–4 days of age (8 hrs), and six nests with chicks 7–9 days of age (20 hrs). We observed both members of the pair at all of these nests. We video recorded each nest throughout incubation during morning (between 0700 and 1100 hrs) and afternoon (between 1500 and 1900 hrs). We video recorded nests only during the morning for the chick stages.

Data Analysis.—We watched the videotapes in the laboratory and identified the gender of the parent, number of times (to the nearest sec) it landed at, entered, exited, and departed from the nest, and activity at the nest (incubation, feeding, or brooding). We measured the length of each activity in those visits where there were two different behaviors (i.e., feeding and brooding). We calculated the frequency of visits to the nest (nest visits/hr) for each parent, average length of the visits (sec), time elapsed between visits (sec), and proportion of time spent incubating eggs, and feeding and brooding chicks.

We used nonparametric statistics for analyses due to lack of normality of the data and small sample sizes of the groups. Statistical analyses were performed using StatView Version 5.0 statistical software (SAS Institute 1998). All *P*-values are two-tailed with alpha (α) set at 0.05. Data are presented as means ± standard errors. We provide confidence intervals when comparisons yield a nonsignificant result because of small sample sizes (Colegrave and Ruxton 2003).

RESULTS

Tawny-bellied Seedeaters.—Females built the nest and incubated the eggs alone. We did not find differences in frequency and length of incubation bouts between morning and afternoon (Wilcoxon Signed Rank tests, frequency: $z = -0.94$, $P = 0.35$, $n = 6$; length: $z = -0.10$, $P = 0.92$, $n = 6$). Females spent 59 ± 5% of the time at the nest including observations of morning and afternoon together; frequency and length of incubation bouts were 2.3 ± 0.2 bouts/hr and 16.5 min

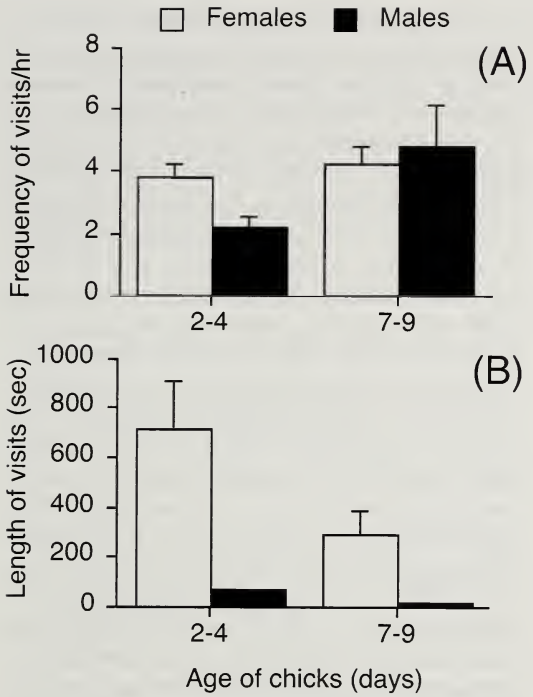


FIG. 1. (A) Frequency and (B) length of nest visits by female and male Tawny-bellied Seedeaters (*Sporophila hypoxantha*) at Reserve El Bagual, Formosa Province, Argentina. Values are mean ± standard errors. The number of nests analyzed was 13 and five for chicks 2–4 and 7–9 days of age, respectively.

± 27 sec, respectively. Males fed females during incubation at three of six nests with a frequency of 0.9 ± 0.5 feedings/hr. Clutch size in nests monitored during incubation was 2.5 ± 0.5 (n = 6 nests).

Females had a higher frequency of nest visits than males when chicks were 2–4 days of age (z = −2.2, P = 0.028, n = 13; Fig. 1). Visits of females were longer than those of males (z = −3.2, P = 0.002, n = 13; Fig. 1); the female remained in the nest brooding the chicks after feeding them on 86% of the visits. Females spent 40 ± 3% of the time brooding chicks while this behavior was not observed in males. The frequency of female's visits with brooding was negatively associated with air temperature (Spearman Rank correlation, ρ = −0.59, z = −2.04, P = 0.042, n = 13), but there was no association between length of brooding visits and air temperature (ρ = 0.19, z = 0.67, P = 0.51, n = 13). The number of chicks in nests monitored at this stage was 1.9 ± 0.5 (n = 13).

There were no gender differences in frequency of nest visits when chicks were 7–9 days of age (z = −0.7, P = 0.50, n = 5, mean ± SD females: 4.2 ± 1.4, males: 4.8 ± 2.9, 95% confidence interval: −3.8 – 2.6; Fig. 1), but females still had significantly longer visits than males (z = −2.0, P = 0.043, n = 5; Fig. 1). Females continued brooding chicks in 21% of the visits and spent 5 ± 2% of the time in this activity; this behavior was not observed in males. The number of chicks in the nests monitored at this stage was 1.6 ± 0.5 (n = 5). Both males and females removed fecal sacs during the chick stage.

Rusty-collared Seedeaters.—Females built the nest and incubated the eggs alone. We did not find differences between morning and afternoon in frequency (z = −0.37, P = 0.72, n = 4) and length (z = −0.0, P = 0.99, n = 4) of incubation bouts. We combined morning and afternoon observations; females spent 51 ± 8% of the time at the nest with a frequency and length of the incubation bouts of 3.0 ± 0.6 bouts/hr and 12.5 ± 3.2 min, respectively. We observed that in one of four nests the male fed the female during incubation (frequency = 0.65/hr). Clutch size in the nests monitored during incubation was 2.7 ± 0.5 (n = 4 nests).

The frequency and length of nest visits when chicks were 2–4 days of age did not differ between genders (z = −0.73, P = 0.46, n = 4, mean ± SD females: 3.1 ± 1.7, males: 1.5 ± 2.1, 95% confidence interval: −2.4 – 5.5; and z = −1.46, P = 0.14, n = 4, mean ± SD females: 263.8 ± 330.8 sec, males: 56.1 ± 75.2 sec, 95% confidence interval: −228.1 – 644.1, respectively, Fig. 2). Females spent 19 ± 15% of the time brooding chicks. The male brooded the chicks in two of four nests. The number of chicks in the nests monitored at this stage was 2.2 ± 0.5 (n = 4).

The frequency of nest visits was higher for females when chicks were 7–9 days of age (z = −2.0, P = 0.046, n = 6; Fig. 2). Females brooded the chicks 13 ± 8% of the time at this stage, while brooding by males was not observed; we did not detect gender differences in length of nest visits (z = −1.4, P = 0.17, n = 6, mean ± SD females: 364.8 ± 617.8 sec, males: 16.7 ± 2.76 sec, 95% confidence interval: −299.3 – 995.5; Fig. 2). The number

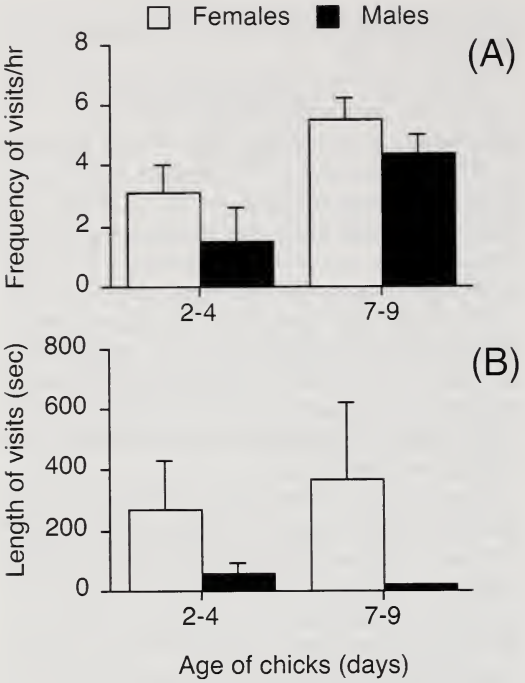


FIG. 2. (A) Frequency and (B) length of nest visits by female and male Rusty-collared Seedeaters (*Sporophila collaris*) at Reserve El Bagual, Formosa Province, Argentina. Values are mean ± standard errors. The number of nests analyzed was four and six for chicks 2–4 and 7–9 days of age, respectively.

of chicks in the nests monitored at this stage was 1.7 ± 0.8 (n = 6). Both males and females removed fecal sacs during the chick stage.

DISCUSSION

Parental care is female biased in Tawny-bellied and Rusty-collared seedeaters. The female built the nest and incubated the eggs without assistance of the male in both species. The pattern of parental care after hatching was also similar between species with females spending more time at the nest than males. The main difference between species was that male Rusty-collared Seedeaters brooded the chicks while this was not observed in Tawny-bellied Seedeaters. Other differences between species (i.e., lack of gender differences in frequency and length of visits in the period of 2–4 days of age in Rusty-collared Seedeaters) could be attributed to low power because of small sample sizes.

There are previous studies in other species of seedeaters that provide some qualitative data on type and extent of parental care including: White-collared Seedeater (*S. morelleti*; Skutch 1954), Slate-colored Seedeater (*S. schistacea*; Stutchbury et al. 1996), Variable Seedeater (*S. corvine*; Gross 1952, Skutch 1954), Lined Seedeater (*S. lineola*; Marcondes-Machado 1997), Yellow-bellied Seedeater (*S. nigricollis*; Alderton 1961), and Double-collared Seedeater (*S. caerulescens*; Francisco 2006). The female incubates the eggs and broods the chicks alone in all of these species and males did not participate in nest building, except for Yellow-bellied Seedeaters. Both parents provision the young in most of these species but there is no information on gender bias in provisioning rates (except for Double-collared Seedeater where females have a higher frequency of nest visits than males, Francisco 2006). The only species where males do not participate in chick feeding is Slate-colored Seedeater (Stutchbury et al. 1996). None of the previous studies reported mate feeding by males during incubation (as we observed in Tawny-bellied and Rusty-collared seedeaters) or male brooding (as we observed in Rusty-collared Seedeater). The results for species of seedeaters studied to date indicate this group has female biased biparental care with noticeable differences in the type and extent of male care.

Plumage coloration often has an important role in conspecific interactions (Andersson 1994); Owens and Hartley (1998) reported gender differences in parental care are associated with melanin-based dimorphism. Eumelanin pigments often signal competitive ability and social dominance (Senar 1999), and act as honest signals of male parental quality in a few species (Siefferman and Hill 2003). We did not study the pigments responsible for plumage coloration, but it is likely the rufous rump and underparts of Tawny-bellied Seedeaters, and the black head, black pectoral band, and cinnamon rump and underparts of Rusty-collared Seedeaters are produced by eumelanins and pheomelanins (Gill 1995). Further studies analyzing preference of females for coloration of males, and the association between coloration of males and parental quality may help in understanding the function of sexual dichromatism in this group.

ACKNOWLEDGMENTS

We thank Alparamis SA and Aves Argentinas/Asociación Ornitológica del Plata for allowing us to conduct this study at Reserve El Bagual. We also thank two anonymous reviewers for helpful comments on a previous version of this manuscript. CF was supported by a fellowship from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). JCR is a Research Fellow of CONICET.

LITERATURE CITED

Alderton, C. C. 1961. The breeding cycle of the Yellow-bellied Seedeater in Panama. Condor 63:390–398.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey, USA.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey, USA.

Colegrave, N. and G. D. Ruxton. 2003. Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. Behavioral Ecology 14:446–450.

Di Giacomo, A. G. 2005. Aves de la Reserva El Bagual. Pages 203–465 *in* Historia Natural y Paisaje de la Reserva El Bagual. Temas de Naturaleza y Conservación 4 (A. G. Di Giacomo and S. F. Krapovickas, Editors). Aves Argentinas/Asociación Ornitológica del Plata, Buenos Aires, Argentina.

Francisco, M. R. 2006. Breeding biology of the Double-collared Seedeater (*Sporophila caerulescens*). Wilson Journal of Ornithology 118:85–90.

Gill, F. B. 1995. Ornithology. W. H. Freeman and Company, New York, USA.

Gross, A. O. 1952. Nesting of Hicks' Seedeater at Barro Colorado Island, Canal Zone. Auk 69:433–446.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen Press, London, United Kingdom.

Lijtmaer, D. A., N. M. M. Sharpe, P. L. Tubaro, and S. C. Lougheed. 2004. Molecular phylogenetics and diversification of the genus *Sporophila* (Aves: Passeriformes). Molecular Phylogenetics and Evolution 33:562–579.

Marcondes-Machado, L. O. 1997. Reproductive behavior of *Sporophila lineola* (Linnaeus) (Passeriformes, Emberizidae). Revista Brasileira de Zoologia 14:517–522.

Meyer de Schauensee, R. 1952. A review of the genus *Sporophila*. Proceedings of the Academy of Natural Sciences of Philadelphia 104:153–196.

Neudorf, D. L. H. 2004. Extrapair paternity in birds: understanding variation among species. Auk 121: 302–307.

Owens, I. P. F. and I. R. Hartley. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proceedings of the Royal Society of London, Series B 265:397–407.

Ridgely, R. S. and G. Tudor. 1989. The birds of South America. Volume 1. Oxford University Press, Oxford, United Kingdom.

SAS Institute. 1998. StatView user's guide. Version 5.0. SAS Institute Inc., Cary, North Carolina, USA.

Senar, J. C. 1999. Plumage coloration as a signal of social status. Proceedings of the International Ornithological Congress 22:1669–1686.

Siefferman, L. and G. E. Hill. 2003. Structural and melanin coloration indicate parental effort and reproductive success in male Eastern Bluebirds. Behavioral Ecology 14:855–861.

Silver, R., H. Andrews, and G. F. Fall. 1985. Parental care in an ecological perspective: quantitative analysis of avian subfamilies. American Zoologist 25:823–840.

Skutch, A. F. 1954. Life histories of Central American birds. Families Fringillidae, Thraupidae, Icteridae, Parulidae and Coerebidae. Pacific Coast Avifauna 31:19–49.

Soler, J. J., A. P. Møller, and M. Soler. 1998. Nest building, sexual selection and parental investment. Evolutionary Ecology 12:427–441.

Stutchbury, B. J. M., P. R. Martin, and E. S. Morton. 1996. Nesting behavior of the Slate-Colored Seedeater (*Sporophila schistacea*) in Panama. Ornitología Neotropical 7:63–65.

Verner, J. and M. F. Willson. 1969. Mating systems, sexual dimorphism and the role of male North American passerine birds in the nesting cycle. Ornithological Monographs 9:1–76.

The Wilson Journal of Ornithology 120(4):884–887, 2008

Postnatal Growth Rates of Hummingbirds: Review and New Records

Bernd P. Freymann[1,2,3] and Karl-Ludwig Schuchmann[1]

ABSTRACT.—We review the published information on postnatal growth rates of hummingbirds (13 species), and report previously unpublished records for nine additional trochilid species. The allometric relationship based on the $\log_{10}$-transformed data of K (logistic growth rate constant) and body mass has a slope of −0.313 and an intercept of −0.346 (n = 22; r^2 = 0.18; P = 0.049). The allometric relationship has a slope of −0.366 and an intercept of −0.327 (n = 20; r^2 = 0.30; P = 0.013) if the two Nearctic records are excluded. Visual inspection suggests that higher K-values occur in Nearctic hummingbirds ($\bar{x}$ = 0.422; n = 2) compared to Neotropic species ($\bar{x}$ = 0.269; n = 20). We suggest a revival of studies collecting basic life history information such as postnatal growth rates of birds, especially of tropical taxa. *Received 12 October 2007. Accepted 18 February 2008.*

The Metabolic Theory of Ecology (MTE) is a controversially debated theory related to search for nomological explanations in ecology (Brown et al. 2004). It represents a revival of allometric scaling studies linking organismal metabolic rates to body mass—across several orders of magnitude—via temperature as the central factor (Gillooly et al. 2001). Gillooly et al. (2002) in the framework of MTE, also developed a fundamental model, based on first principles of allometry and biochemical kinetics, that predicts the time of ontogenetic development as a function of body mass (bm) and temperature. Their model focuses on embryonic growth but is, to a certain extent, also applicable to postnatal growth (Gillooly et al. 2002). The discussion of MTE indicates that raw data on life history aspects such as postnatal growth rates of single and, in particular, tropical taxa, are still sparse and urgently needed. Hummingbirds (Trochilidae), which are predominantly nectarivorous, lay invariably two eggs in nests that are mostly of cup-like, occasionally also domed or semi-domed, architecture (Schuchmann 1999). After an incubation period of 16–19 days the altricial chicks stay for another 23–26 days, in case of the high Andean trochilids 30–40 days, in the nest (Schuchmann 1999). The nestlings are fed by regurgitation of fluid and arthropods, often spiders (e.g., Thomas 1994, Marín 2001). We report previously unpublished records of postnatal growth rates of hummingbirds and review the published records of this family. We show how this information applies to important ecological questions, e.g., temperate versus tropical growth rates.

METHODS

New Records.—The previously unpublished data on postnatal growth rates of hummingbirds presented here were measured by the senior author and Julia Beintmann (1998) during 1984–2004 at a variety of localities (Table 1).

We obtained growth constants (K) for nestlings using the logistic equation provided by Ricklefs (1976):

$$W_t = A \times (1+e^{-K\,(t-t_i)})^{-1}$$

where W_t = mass at time t; A = maximum mass; e = base of the natural logarithms; K = growth rate constant; and t_i = age at the inflection point of the growth curve. An inverse measure of growth, the time required to grow from 10 to 90% of the asymptote (Ricklefs 1976) was calculated using the equation:

$$t_{10-90}\ (\text{days}) = 4.4/K.$$

Literature Review.—We searched the literature for published records starting with the avian growth rate data set from Starck and Ricklefs (1998). K- and t_{10-90}-values were either from the original publications or computed by us using the formulas from Ricklefs

[1] Alexander Koenig Research Institute and Museum of Zoology (ZFMK), Leibniz Institute for Terrestrial Biodiversity, Research Group: Biology and Phylogeny of Tropical Birds, Adenauerallee 160, 53113 Bonn, Germany.

[2] Current address: Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P. O. Box 14, 9750 AA Haren, The Netherlands.

[3] Corresponding author; e-mail: b.freymann@rug.nl

TABLE 1. Postnatal growth rates of hummingbirds (Trochilidae). K = growth rate, n = individuals measured, t_{10-90} = inverse growth rate.

Subfamily Species	Body mass [g]	K [d^{-1}]	t_{10-90} [d]	n	Locality (altitude [m])	Reference
Phaethornithinae						
Ramphodon naevius	6.9[a]	0.206	21.4	2	Brazil (650)	This study
Glaucis hirsuta	6.8[a]	0.251	17.5	1	Trinidad (500)	This study
Phaethornis ruber	2.4	0.469	9.4	1	Surinam (50)	Schuchmann 1986
Trochilinae						
Campylopterus hemileucurus	10.3	0.148[b]	14.6	7	Costa Rica (1,900)	Marín 2001
Colibri coruscans	7.7	0.29	15.2	5	Ecuador (3,000)	Beintmann 1998
		0.300	14.7	8	Venezuela (4,000)	Züchner 1998
Eulampis jugularis	9.5[a]	0.273	16.1	3	St. Lucia (900)	This study
Orthorhyncus cristatus	3.8[a]	0.270	16.3	2	Guadeloupe (150)	This study
Chlorostilbon mellisugus	2.8	0.278	15.8	1	Venezuela (700)	Thomas 1994
Thalurania colombica	4.2[a]	0.322	13.7	1	Colombia (500)	This study
Amazilia tzacatl	5.0	0.362	12.1	2	Panama (50)	Ricklefs 1976
		0.334	13.2	3	Colombia (500)	Schuchmann and Tögel *in* Starck and Ricklefs 1998
Polyerata fimbriata	5.2	0.256	17.2	1	Surinam (s.l.)	Haverschmidt 1952
Saucerottia tobaci	4.4[a]	0.264[b]	16.7	2	Trinidad (s.l.)	Muir 1925
Lampornis clemenciae	7.5	0.463	9.5	2	USA (1,650)	Schuchmann 1985
Sternoclyta cyanopectus	6.8	0.28	15.7	10	Venezuela (1,350–2,000)	Fierro-Calderón and Martin 2007
Oreotrochilus estella	8.0	0.190[b]	23.2	2	Peru (3,900)	Dorst 1962
Haplophaedia lugens	5.9	0.172	25.6	2	Colombia (1,800)	This study
Ocreatus underwoodii	2.9[a]	0.195	22.6	1	Colombia (1,800)	This study
Lesbia victoriae	5.1	0.25	17.6	5	Ecuador (3,100)	Beintmann 1998
Oxypogon guerinii	5.5	0.233	18.9	6	Venezuela (4,000)	Züchner 1998
Metallura tyrianthina	3.8	0.27	16.3	6	Ecuador (3,100)	Beintmann 1998
Calliphlox evelynae	3.3	0.408	10.8	2	Bahamas (s.l.)	Schuchmann *in* Starck and Ricklefs 1998
Selasphorus rufus	3.5	0.380	11.6	2	USA (600)	Constantz 1980

[a] Source not original publication but Schuchmann (1999); if available mean of males and females given.
[b] Data newly computed.

(1976). Missing data on adult body mass not reported in the original publications are from Schuchmann (1999).

Statistical Analysis.—We $\log_{10}$-transformed the raw data for body mass (g) and K prior to analysis. We used least-squares regression (GLM) in Statistica 6.1 (StatSoft 2003) to test whether body mass predicts K (assuming independence among the data).

RESULTS

We obtained published information on K- and t_{10-90}-values for 13 trochilid species from the literature (Table 1). We also present previously unpublished data on the postnatal growth parameters of nine additional hummingbird species (Table 1). This increases the number of hummingbird species (n = 20) with published information on K- and t_{10-90}-values by 69%: the number of published records rises from one to three for the subfamily Phaethornithinae. We also present an additional record for one previously reported species (Table 1).

The allometric relationship based on the $\log_{10}$-transformed data of K and body mass (g) has a slope of −0.313 and an intercept of −0.346 (n = 22; r^2 = 0.18; P = 0.049) for all species included. The allometric relationship has a slope of −0.366 and an intercept of −0.327 (n = 20; r^2 = 0.30; P = 0.013) if the two Nearctic records (*Lampornis clemenciae* and *Selasphorus rufus*) are excluded. A statistical comparison of the means of the K-values of the Nearctic versus Neotropic hum-

mingbird species is not meaningful due to small sample sizes, but visual inspection suggests that higher *K*-values occur in Nearctic hummingbirds ($\bar{x}$ = 0.422; n = 2) compared to the neotropical trochilids ($\bar{x}$ = 0.269; n = 20).

DISCUSSION

Our synthesis of previously unreported as well as published records represents a significant quantitative and qualitative improvement of the information available on postnatal growth development of juvenile hummingbirds. The quantitative improvement is apparent at first glance, given the increase of records by 69%. The qualitative improvement is more obscure. The most complete review of postnatal growth rates was published by Starck and Ricklefs (1998). The newer work by Fierro-Calderón and Martin (2007) on the Violet-chested Hummingbird (*Sternoclyta cyanopectus*) is a detailed and informative study on the reproductive biology of this species. It also includes a review and discussion of several reproductive parameters of hummingbirds comparing tropical with temperate species.

A reanalysis of Starck and Ricklef's (1998) data set on trochilids yields the following allometric relationships between *K* (y) and body mass (x): $y = -0.154x - 0.382$ (n = 10; r^2 = 0.06; P = 0.51 for all species) and $y = -0.360x - 0.281$ (n = 8; r^2 = 0.33; P = 0.14 excluding the Nearctic species). A slight increase in data quality due to increased sample size is apparent in case of the joint analysis of all species together (r^2 = 0.18 vs. r^2 = 0.06). Our value for the slope of the allometric relationship of −0.366 (excluding Nearctic species) closely resembles the overall value reported for 557 bird species of −0.316 (Starck and Ricklefs 1998), but is considerably lower than those reported by the same authors for other altricial taxa (Columbiformes = −0.26, Psittaciformes = −0.18, Piciformes = −0.17, Passeriformes = −0.15). A separate analytical treatment of the Neotropic versus Nearctic hummingbird species resulted in a significant improvement of the fit of the regression lines. Visual inspection suggests that higher *K*-values occur in Nearctic hummingbirds compared to the Neotropic species.

These findings support the hypothesis by Ricklefs (1968, 1976) that tropical passerines grow more slowly than passerines from temperate regions is also valid for hummingbirds. Questions concerning the ultimate mechanisms underlying this observation remain unanswered (e.g., different predation pressures on temperate vs. tropical hummingbirds). Ricklefs (1968, 1976) discussed the factors of different day length and basal metabolic rate. While the first model holds for tropical versus temperate taxa in Ricklefs' data set, it could not be extended to the comparison with arctic bird species. However, Ricklefs found that basal metabolism was 25% lower in tropical taxa compared to the studied temperate species. We note that our mean *K*-value for Nearctic hummingbirds ($\bar{x}$ = 0.422; n = 2) closely resembles that for some nectarivorous sunbirds (Nectariniidae) ($\bar{x}$ = 0.417; n = 3) (Earlé 1982, Goldstein and Yom-Tov 1988, Maher 1991, reviewed in Starck and Ricklefs 1998), while that of the neotropical trochilids ($\bar{x}$ = 0.269; n = 20) does not.

This study provides important, new information on postnatal growth rates of hummingbirds. There is an obvious lack of data on this topic and we suggest not only a revival of allometric scaling studies, but a revival of studies (e.g., Fierro-Calderón and Martin 2007) collecting basic life history information on postnatal growth rates of birds, especially of tropical taxa.

ACKNOWLEDGMENTS

We are indebted to C. E. Braun, Roland Prinzinger, and two anonymous referees for their insightful criticism and careful reviews of an earlier version of the manuscript. BPF is grateful to Sara Nelly de Visser for encouragement, to Stefanie Rick, ZFMK, Ornithological Library, for assistance with acquisition of literature, and to the German National Merit Foundation (Studienstiftung des Deutschen Volkes) and e.fellows.net for financial support. KLS acknowledges the Brehm Fund for International Bird Conservation for funding Julia Beintmann's thesis and a grant from the German National Council to conduct field work in Ecuador (Schu/766/5-3, 5-4, 5-5).

LITERATURE CITED

Beintmann, J. 1998. Vergleichende Reproduktionsbiologie dreier Kolibriarten (Trochilidae) *Lesbia victoriae*, *Metallura tyrianthina* und *Colibri coruscans* in den Anden Ecuadors. Thesis. Rheinische Friedrich-Wilhelms-Universität, Bonn, Germany.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Sav-

AGE, AND G. B. WEST. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

CONSTANTZ, G. D. 1980. Growth of nestling Rufous Hummingbirds. Auk 97:622–624.

DORST, J. 1962. Nouvelles recherches biologiques sur le trochilidés des hautes andes Pèruviennes (*Oreotrochilus estella*). L'Oiseau 32:95–126.

EARLÉ, R. A. 1982. Aspects of the breeding biology of the Whitebellied Sunbird. Ostrich 53:65–73.

FIERRO-CALDERÓN, K. AND T. E. MARTIN. 2007. Reproductive biology of the Violet-chested Hummingbird in Venezuela and comparisons with other tropical and temperate hummingbirds. Condor 109:680–685.

GILLOOLY, J. F., J. H. BROWN, G. B. WEST, V. M. SAVAGE, AND E. L. CHARNOV. 2001. Effects of size and temperature on metabolic rate. Science 293: 2248–2251.

GILLOOLY, J. F., E. L. CHARNOV, G. B. WEST, V. M. SAVAGE, AND J. H. BROWN. 2002. Effects of size and temperature on developmental time. Nature 417:70–73.

GOLDSTEIN, H. AND Y. YOM-TOV. 1988. Breeding biology of the Orange-tufted Sunbird in Israel. Ardea 76:169–174.

HAVERSCHMIDT, F. 1952. Notes on the life history of *Amazilia fimbriata* in Surinam. Wilson Bulletin 64:69–79.

MAHER, W. J. 1991. Growth and development of the Yellowbellied Sunbird, *Nectarinia jugularis*, in North Queensland. Emu 91:58–61.

MARÍN, M. 2001. Postnatal development of the Violet Sabrewing in Costa Rica. Wilson Bulletin 113: 110–114.

MUIR, A. 1925. The nesting of the Emerald Hummingbird (*Saucerottia tobaci erythronota*) in Trinidad. Ibis 67:648–654.

RICKLEFS, R. E. 1968. Patterns of growth in birds. Ibis 110:419–451.

RICKLEFS, R. E. 1976. Growth rates of birds in the humid New World tropics. Ibis 118:179–207.

SCHUCHMANN, K.-L. 1985. Morpho- und Thermogenese nestjunger Blaukehlkolibris (*Lampornis clemenciae*). Journal für Ornithologie 126:305–308.

SCHUCHMANN, K.-L. 1986. Natal care and growth in a nestling Reddish Hermit (*Phaethornis ruber*) in Surinam. Ardea 74:101–104.

SCHUCHMANN, K.-L. 1999. Family Trochilidae (Hummingbirds). Pages 468–680 *in* Handbook of the birds of the world. Volume 5. Barn-owls to hummingbirds (J. del Hoyo, A. Elliot, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

STARCK, J. M. AND R. E. RICKLEFS. 1998. Avian growth rate data set. Pages 381–423 *in* Avian growth and development (J. M. Starck and R. E. Ricklefs, Editors). Oxford University Press, New York, USA.

STATSOFT INC. 2003. STATISTICA. Version 6.1. StatSoft Inc., Tulsa, Oklahoma, USA.

THOMAS, B. T. 1994. Blue-tailed Emerald Hummingbird (*Chlorostilbon mellisugus*) nesting and nestling development. Ornitologia Neotropical 5:57–60.

ZÜCHNER, T. 1998. Reproductive patterns of two hummingbird species at high elevation in the Venezuelan Andes. Ostrich 69:341.

The Wilson Journal of Ornithology 120(4):887–890, 2008

Begging Behavior of Fledgling Rusty-breasted Cuckoo (*Cacomantis sepulcralis*)

Tomáš Grim[1]

ABSTRACT.—I describe previously unknown begging calls and displays of a fledgling Rusty-breasted Cuckoo (*Cacomantis sepulcralis*) fed by a Pied Fantail (*Rhipidura javanica*) in Singapore. The cuckoo emitted two types of begging calls: (1) 'host-absent begging call' (loud 'tsi' repeated at 1-sec intervals) and (2) 'standard' begging call in the presence of the Pied Fantail (wheezy 'seeee' repeated 1–2 times/sec). The fledgling also performed the 'wing-shake begging' display, i.e., it raised one of its wings at a time towards the approaching Pied Fantail. This display was similar to that of the best studied brood parasite, the Common Cuckoo (*Cuculus canorus*). The structure of both types of begging calls of the Rusty-breasted Cuckoo was different in comparison to the Common Cuckoo and relatively more similar to some other closely related species of the genus *Cacomantis*. *Received 2 October 2007. Accepted 9 February 2008.*

The biology and ecology of brood parasitic cuckoos has received major attention during the last two decades (Davies 2000). However, most data are from only one species, the Common Cuckoo (*Cuculus canorus*). The knowl-

[1] Department of Zoology, Palacky University, tr. Svobody 26, CZ-771 46 Olomouc, Czech Republic; e-mail: tomas.grim@upol.cz

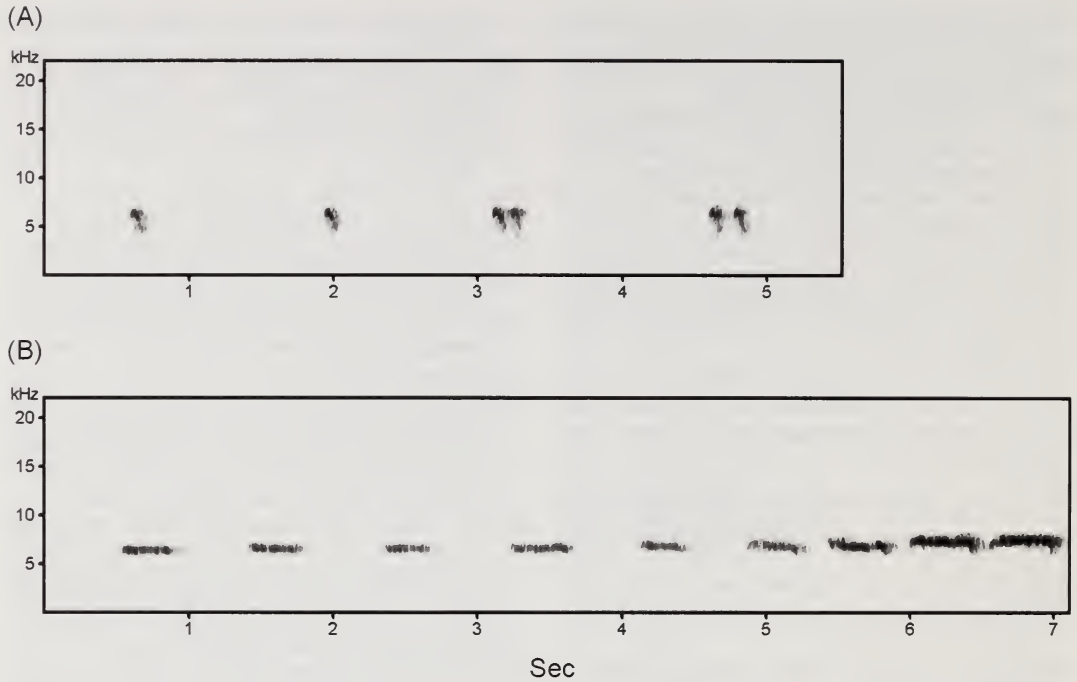


FIG. 1. Sonagrams of begging calls of fledgling Rusty-breasted Cuckoo in the absence of the Pied Fantail (A) and during its presence (B). The sonagrams were created using AVISOFT software and the background noise (cicada calls) was cleaned.

edge of even the general biology of other species is extremely poor, especially at the chick and fledgling stages (Grim 2006, 2007). This is true for most tropical brood parasites and in agreement with the poorly known biology of tropical birds in general (Martin 1996). Therefore, I report an observation of previously undescribed begging calls and begging behavior of a tropical cuckoo.

OBSERVATIONS

I observed a Pied Fantail (*Rhipidura javanica*) feeding a fledgling Rusty-breasted Cuckoo (*Cacomantis sepulcralis*) on 11 August 2007 in Sungei Buloh Wetland Reserve, Singapore. I localized the fledgling in the mangrove (*Rhizophora* sp., *Avicennia* sp.) habitat by its loud begging call. When the Pied Fantail was not present the cuckoo emitted the 'host-absent begging call'. This was a relatively loud 'tsi', about 0.1 sec in duration, 4–7 kH, repeated at 1/sec intervals (Fig. 1A left). At times the fledgling produced a doubled 'tsi' call (Fig. 1A right). The fledgling dramatically changed the structure of calling when the Pied Fantail approached and it produced the 'standard begging call'. This was a wheezy 'seeee', about 0.3–0.5 sec in duration at 6–7 kH. The cuckoo repeated the call at 1/sec intervals and increased in both rate (to 2 calls/sec) and frequency (to 7–8 kH) when the Pied Fantail was at close range (several cm from the chick) (Fig. 1B).

The Rusty-breasted Cuckoo fledgling sat on a branch 2 m above ground level and changed the perch only once during my observations. I observed the cuckoo chick from a distance of ~7 m for a period of ~10 min during which it was fed five times by the Pied Fantail. The cuckoo started to beg at a faster rate when it observed the approaching fantail. It also showed the 'wing-shake begging'. During this display the chick raised its wing at an angle of ~90° above horizontal and towards an approaching fantail. The display of the Rusty-breasted Cuckoo was *asymmetric*, i.e., the chick raised only one wing at the time. The fledgling in all five cases of feedings raised vertically the wing towards the approaching fantail (right wing 3 times, left

wing 2 times). In one case the fantail started to approach from the right side of the chick but finally arrived at the left side; the cuckoo synchronously changed the raised right wing for the raised left one. The chick stopped the wing-shake begging display when the fantail left the area. I saw only one fantail at the time but cannot exclude the possibility that two birds actually fed the chick. I was unable to identify the prey fed by the fantail to the cuckoo.

DISCUSSION

Cuckoo fledglings are occasionally fed by adults that did not raise them or even by species that do not raise cuckoos (Sealy and Lorenzana 1997), but the Pied Fantail was previously reported as a regular host of the Rusty-breasted Cuckoo in Java (Payne 2005). However, the hosts of this cuckoo in Malay Peninsula were 'not identified' (Wells 1999: 387). Some 60 passerine species have been recorded as hosts of the Rusty-breasted Cuckoo (Payne 2005).

The information on Rusty-breasted Cuckoo breeding biology is sparse. Johnsgard (1997: 215) reports 'No information' and Payne (1997) provides no data on cuckoo behavior in the postfledging period. Wells (1999: 387) reports 'No information' on the breeding behavior of the Rusty-breasted Cuckoo while Brooker and Brooker (1989) mention the fledging period is ~19 days. Payne (2005: 447) provides more details; he reports that one of three egg morphs of the Rusty-breasted Cuckoo mimics eggs of fantails (*Rhipidura* spp.), the nestling cuckoo evicts host eggs and young, the nestling period is 17–19 days, and the length of the post-fledging care is 1 month.

The compendium by Payne (2005) describes begging behavior by other cuckoo species, but mentions only a few records of Rusty-breasted Cuckoo fledglings and virtually no information on their calls or behavior. Higgins (1999: 682) reports 'no information on calls of nestlings' in the closely related Brush Cuckoo (*Cacomantis variolosus*). Brooker and Brooker (1989), and Payne (1997, 2005) treated the Rusty-breasted Cuckoo as a subspecies of the Brush Cuckoo.

There is some information on begging calls of two closely related cuckoo congeneric species. The begging call of a juvenile Chestnut-breasted Cuckoo (*C. castaneiventris*) is 'a repeated high-pitched thin wheezy *siiiaar-swee-sweep*' (Higgins 1999: 690). Fully fledged young Fan-tailed Cuckoos (*C. flabelliformis*) begged from a host with 'plaintive almost cicada-like *zeep-zeep-zeep*' (Higgins 1999: 698). These descriptions seem similar to the 'standard begging call' of the Rusty-breasted Cuckoo fledgling (wheezy 'seeee'). However, I have no information on age, gender or hunger level of the cuckoo chicks and any comparisons are only preliminary. It would be interesting to compare the fledgling's call with that of its putative fosterer's own chicks but I was unable to find any information on begging calls of Pied Fantail nestlings (Boles 2006, Wells 2007).

The Rusty-breasted Cuckoo fledgling uttered a different call when the Pied Fantail was absent ('tsi'; Fig. 1A). I found only one description of a 'host-absent begging call' in the literature for cuckoos. Sicha et al. (2007) described the 'host-absent vocalization' of the Common Cuckoo as distinct 'si' sounds repeated at intervals of 0.5–5 sec (Sicha et al. 2007: Fig. 1). The host-absent begging call of the Common Cuckoo has a higher frequency (7–8 kH) than that of the Rusty-breasted Cuckoo (4–7 kH) but sounds relatively similar to the human ear (pers. obs. of both cuckoo species). In contrast, the 'standard begging call' (in the presence of fosterers) of the Common Cuckoo chick spans a much wider range of frequencies (5–10 kH) than that of the Rusty-breasted Cuckoo (6–7 kH) and has a strikingly higher rate (10–20 vs. 1–2 calls/sec). There may be important species differences in the call structure between the two taxa and I acknowledge that differences may arise from factors unrelated to species identity (e.g., age, developmental stage, actual hunger level).

The Rusty-breasted Cuckoo fledgling also performed a 'wing-shake begging' display. This begging strategy seems to be universal in birds (Grim 2008) and the unusual aspect of this behavior in the observed cuckoo species was that the display was asymmetric (i.e., only one wing was raised at a time). Asymmetric wing shaking has also been observed in other cuckoo species (Tanaka and Ueda 2005, Tanaka et al. 2005, Grim 2008). In contrast, passerine chicks raise both wings at a time as a rule (Grim 2008).

Observations on behavior are valuable and indispensable for understanding the basic breeding biology of cuckoos and brood parasite–host interactions. Additional information will be valuable to facilitate cross-species comparisons. I encourage ornithologists and birdwatchers that may have observations on both chicks and fledglings of non-European cuckoos to publish their observations.

ACKNOWLEDGMENTS

I am grateful to Vaclav Pavel for preparing the sonograms. I thank Human Frontier Science Program Organization for supporting my brood parasitism research (grant HFSP RGY69/2007) and to Dana Campbell for correcting the language.

LITERATURE CITED

Boles, W. E. 2006. Family Rhipiduridae (fantails). Pages 200–242 *in* Handbook of the birds of the world. Volume 11. Old World flycatchers to Old World warblers (J. del Hoyo, A. Elliott, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Brooker, M. G. and L. C. Brooker. 1989. Cuckoo hosts in Australia. Australian Zoological Reviews 2:1–67.

Davies, N. B. 2000. Cuckoos, cowbirds and other cheats. T & A. D. Poyser, London, United Kingdom.

Grim, T. 2006. The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? Evolutionary Ecology Research 8:785–802.

Grim, T. 2007. Equal rights for chick brood parasites. Annales Zoologici Fennici 44:1–7.

Grim, T. 2008. Wing-shaking and wing-patch as nestling begging strategies: their importance and evolutionary origins. Journal of Ethology 26:9–15.

Higgins, P. J. (Editor). 1999. Handbook of Australian, New Zealand and Antarctic birds. Volume 4 (Parrots to Dollarbird). Oxford University Press, Melbourne, Australia.

Johnsgard, P. A. 1997. The avian brood parasites. Oxford University Press, New York, USA.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? Journal of Avian Biology 27:263–272.

Payne, R. B. 1997. Family Cuculidae (cuckoos). Pages 508–607 *in* Handbook of the birds of the world. Volume 4. Sandgrouse to cuckoos (J. del Hoyo, A. Elliott, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

Payne, R. B. 2005. The cuckoos. Oxford University Press, New York, USA.

Sealy, S. G. and J. C. Lorenzana. 1997. Feeding of nestling and fledgling brood parasites by individuals other than the foster parents: a review. Canadian Journal of Zoology 75:1739–1752.

Sicha, V., P. Prochazka, and M. Honza. 2007. Hopeless solicitation? Host-absent vocalization in the Common Cuckoo has no effect on feeding rate of Reed Warblers. Journal of Ethology 25:147–152.

Tanaka, K. D. and K. Ueda. 2005. Horsfield's Hawk-Cuckoo nestlings simulate multiple gapes for begging. Science 308:653–653.

Tanaka, K. D., G. Morimoto, and K. Ueda. 2005. Yellow wing-patch of a nestling Horsfield's Hawk Cuckoo *Cuculus fugax* induces miscognition by hosts: mimicking a gape? Journal of Avian Biology 36:461–464.

Wells, D. R. 1999. The birds of the Thai-Malay Peninsula. Volume I. Non-passerines. Christopher Helm, London, United Kingdom.

Wells, D. R. 2007. The birds of the Thai-Malay Peninsula. Volume II. Passerines. Christopher Helm, London, United Kingdom.

The Wilson Journal of Ornithology 120(4):891–897, 2008

Natural History of the Red Owl (*Tyto soumagnei*) in Dry Deciduous Tropical Forest in Madagascar

Scott G. Cardiff[1,3,4] and Steven M. Goodman[2]

ABSTRACT.—Recent observations of the Red Owl (*Tyto soumagnei*) in Madagascar demonstrated that it inhabits dry deciduous forest, and roosts on rock ledges and in cave entrances in the extreme north of the island. We observed a Red Owl at a sinkhole site in the Réserve Spéciale d'Ankarana, found evidence of its use of an additional cave, and collected its pellets in three separate dry seasons between 2000 and 2003. Tsingy tufted-tailed rats (*Eliurus antsingy*) constituted almost 50% of the total prey mass of Red Owls at Ankarana. Their diet at Ankarana differed from that of Red Owls from Masoala in the humid northeast of Madagascar, as the Ankarana pellets contained insects, frogs, and numerous geckos. Red Owls appear to consume more native than introduced rodents and do not appear to prey upon birds or bats like other large owls on the island. Forest degradation could reduce densities of tufted-tailed rats and could be a conservation threat to this owl. *Received 30 May 2006. Accepted 7 February 2008.*

The Red Owl (*Tyto soumagnei*) is rare, endemic to Madagascar and was not observed by biologists for several decades (Thorstrom and Rene de Roland 2003). It is considered "Endangered" (IUCN 2006) and was thought to occur only in humid forests in the east (Grandidier 1878, Halleux and Goodman 1994, Goodman et al. 1996, Thorstrom et al. 1997, ZICOMA 1999, Irwin and Samonds 2002). Limited diet studies suggest the owl feeds on frogs, geckos, afrosoricidans (*Microgale* spp., *Oryzorictes hova*), rodents (*Eliurus* spp., *Rattus rattus*), and the eastern rufous mouse lemur (*Microcebus rufus*) (Lavauden 1932, Halleux and Goodman 1994, Goodman and Thorstrom 1998). These different prey animals are native to Madagascar with the exception of the roof rat (*Rattus rattus*). Until recently, observers have noted owls roosting only in trees in intact and degraded humid forest (Thorstrom and Rene de Roland 1997, Thorstrom et al. 1997, Irwin and Samonds 2002).

Cardiff and Befourouack (2003) and Van Esbroeck (2006) extended the known range of the owl to Ankarana in the north of the island. Van Esbroeck (2006) observed Red Owls at Ankarana in 1999; that observation represents the first record of the occurrence of this owl in dry deciduous forest and the first record of it roosting in a cave entrance or rocky crevice. Our observation of a Red Owl at Ankarana in 2000 (Cardiff and Befourouack 2003) prompted us to obtain further information on the distribution, diet, and roosting habits of this poorly known species and its congener, the Barn Owl (*T. alba*) at Ankarana.

METHODS

The Réserve Spéciale d'Ankarana, ~60 km south of Antsiranana in northern Madagascar (Fig. 1) (12° 49′ to 13° 01′ S and 49° 00′ to 49° 16′ E), encompasses a massif of Jurassic limestone with dry deciduous forest partially surrounded by and intruded upon by semi-deciduous forest (Cardiff and Befourouack 2003). Precipitation near the reserve averages 180–200 cm per year (Rossi 1976, Hawkins et al. 1990). The local limestone karst features many caves and several river sinkholes (Radofilao 1977). These include, on the east side of the reserve, a large collapse sinkhole (collapse doline), where Van Esbroeck (2006) observed a Red Owl in 1999 at the Perte des Rivères, which is also known as the Perte de la Besaboba Number 1 (Radofilao 1977; J.

[1] Columbia University, Department of Ecology, Evolution, and Environmental Biology, 1200 Amsterdam Avenue, New York, NY 10027, USA, and Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA.

[2] Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA, and Vahatra, BP 3972, Antananarivo (101), Madagascar.

[3] Current address: 1331 Pinewood Drive, Pittsburgh, PA 15243, USA.

[4] Corresponding author; e-mail: sgc2102@columbia.edu

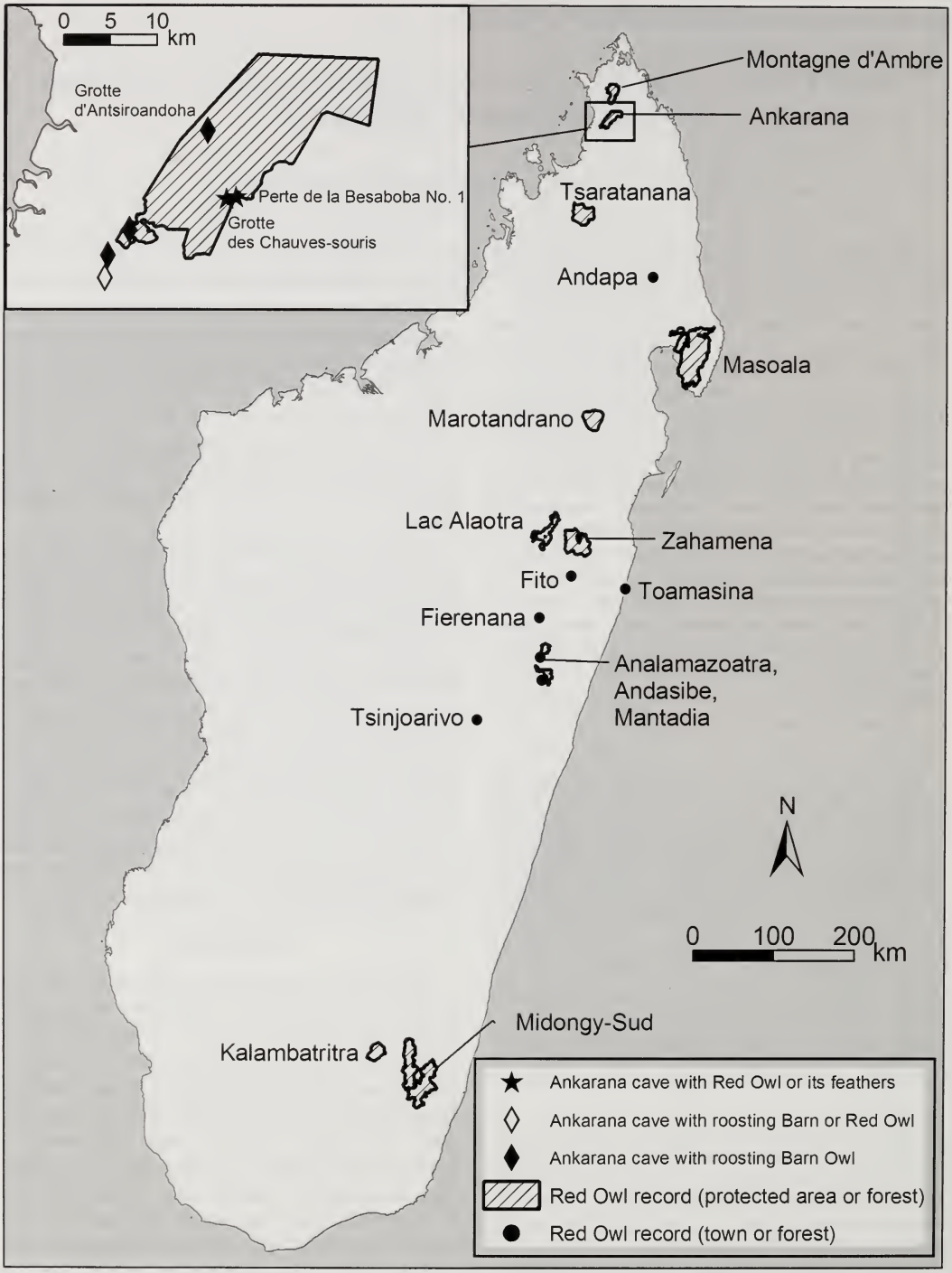


FIG. 1. Recorded distribution of *Tyto soumagnei* on Madagascar and in Ankarana, and distribution of *Tyto alba* at Ankarana.

Radofilao, unpubl. data) and "Perte des trois rivières" (Van Esbroeck 2006). Savannah occurs within ~200 m and semi-deciduous forest on basalt occurs within 500 m of this sinkhole site.

We recorded the presence or absence of all owl species seen or heard at 28 caves from 2003 to 2006 in and around Ankarana during cave biological inventory and monitoring work (Cardiff 2006). We made additional observations at the Perte des Rivières site in the 2000, 2001, and 2003 dry seasons between June and November. We noted the presence of pellets and checked potential roost positions for owls on several occasions to understand roost characteristics and periodicity of roost occupation in 2000 and 2001, and also collected pellets in 2003. We collected >45 pellets and pellet fragments at this site over the three dry seasons. We assumed that all pellets found at the site were from Red Owls based on the concurrent observation of an individual present or feathers attributable to the species on two of three collection dates in 2000 and on two of five dates in 2001. We also collected broken pellets at the entrances of the Grotte d'Antsironandoha on the western side of Ankarana. We attributed pellets collected at Grotte d'Antsironandoha to Barn Owls because we observed a Barn Owl at this location. We did not conduct formal inventories for owls in forests away from cave entrances.

We measured the dimensions of several intact pellets and identified prey items in all collected material. We washed the pellet contents through a sieve after soaking pellets in soapy water and identified recovered hard items to species or species group using collections material at the Field Museum of Natural History in Chicago. We counted the minimum number of individuals (MNI) by the number of unique bilateral elements for each species or species group (Goodman et al. 1991), and calculated relative contribution to total number of individuals and relative contribution to total prey mass based on reference prey masses (Marti 1987).

RESULTS

Distribution.—We observed *Tyto* spp. at five of 28 caves. Three of those observations were of a Barn Owl and one was not identified to species. We only observed Red Owls at the Perte des Rivières, but we also observed and photographed a feather of a Red Owl in 2006 at the entrance to the Grotte des Chauves-souris ("Andavampanihy"), a large cave 1 km west of the Perte des Rivières.

Roosting Habits.—On 31 July 2000 at 0800 hrs, SGC observed one Red Owl on a ledge in a crack in the limestone below the overhang of the edge of the Perte des Rivières sinkhole. SGC again observed one individual at the same location on 6 August 2000 and again on 3 September 2000. SGC subsequently observed an owl at the site on 1 July 2001 and 5 August 2001 but on different rock ledges. Feathers of Red Owls were also present with collected pellets on 12 November 2000. We did not detect the owl at this site during 16 additional visits in 2000–2001.

The Red Owl was roosting in the general area of the opening to the lower passage in the sinkhole in all observations. The owl was in a fissure about 0.5 × 0.5 m in the ceiling (~8 m from the floor) in front of the entrance to the horizontal passage under the overhang when observed in 2000. Guides had reportedly previously seen two Red Owls together at this location. The owl was roosting on the first occasion in 2001 on a ledge about 3 m above the cave floor and 5 m into the horizontal passage. On another occasion, it was roosting in a small opening on the side of the sinkhole at the entrance to the horizontal passage, ~1.5 m above the floor.

Food Habits.—Four intact Red Owl pellets measured 35 × 24, 40 × 24, 41 × 32, and 58 × 29 mm (length × width). Pellets contained a minimum number of individuals (MNI) of 172 insects, frogs, geckos, and mammals (Table 1). Mammals constituted the greatest proportion of the prey items by individual and by mass for all years with geckos being important in 2000. Frogs, a primate, and insects were present in the pellets in some years but not in others (Table 1). The Madagascan pygmy shrew (*Suncus madagascariensis*) contributed most to the MNI in 2001 and the roof rat contributed up to 27% of the total prey biomass in a given year. Tsingy tufted-tailed rats (*Eliurus antsingy*) contributed the most of any single prey item to prey mass in all years and to prey total MNI in 2000 and 2003 (Table 1).

Barn Owl Pellets from Grotte d'Antsironandoha contained frogs (MNI = 4), birds (*Turnix nigricollis*, MNI = 1; *Foudia*

TABLE 1. Relative importance of tsingy tufted-tailed rats as prey items of one or more Red Owls at Ankarana, Madagascar based on regurgitated pellet samples from three different years. Possible frog and gecko prey species identification is based on records of herpetological collections (A. Raselimanana and M. Razafimpahanana, unpubl. data; C. Raxworthy, unpubl. data). PN = number of entire pellets (* additional fragments also examined). MNI = Minimum Number of Individuals.

		Collection year (and months), collection totals, and percent of totals for prey items							
		2000 (Sep–Nov) PN = 8* MNI = 30		2001 (Jun–Sep) PN = 25 MNI = 90		2003 (Jun–Jul, Nov) PN = 12* MNI = 52		All years combined PN = 45* MNI = 172	
Prey item	Mass (g)	MNI (%)	Mass (%)	MNI (%)	Mass (%)	MNI (%)	Mass (%)	MNI (%)	Mass (%)
Insecta				8.9	0.8	5.8	0.8	6.4	0.6
Coleoptera	~4[h]			2.2	0.3	3.8	0.4	2.3	0.2
Dictyoptera: Blaberidae[a]	7.5[i]					1.9	0.4	0.6	0.1
Orthoptera	~2.5[h]			6.7	0.5			3.5	0.2
Amphibia: Anura						17.3	2.8	5.2	0.8
Large[b]	~9.5[j]					5.8	1.5	1.7	0.4
Medium[c]	~4.5[k]					7.7	1.0	2.3	0.3
Small[d]	~3.0[j]					3.8	0.3	1.2	0.1
Squamata: Gekkonidae			19.8	24.4	24.3	28.8	26.7	27.9	23.8
Large[e]	~50[l]	10.0	8.4	7.8	11.7	7.7	10.6	8.1	10.5
Medium[f]	~29[m]	20.0	9.7	12.2	10.6	19.2	15.3	15.7	11.7
Small[g]	~15[l]	6.7	1.7	4.4	2.0	1.9	0.8	4.1	1.6
Mammalia		63.3	80.2	66.7	74.9	48.1	69.7	60.5	74.9
Soricomorpha		10.0	0.4	36.7	2.5	17.3	1.5	26.2	1.7
Suncus madagascariensis	2.3[k]	10.0	0.4	36.7	2.5	15.4	1.0	25.6	1.5
Afrosoricida						1.9	0.6	0.6	0.2
Microgale brevicaudata	10.7[l]					1.9	0.6	0.6	0.2
Rodentia		53.3	79.9	30.0	72.4	25.0	58.5	32.6	70.5
Eliurus antsingy	87.5[l]	46.7	68.4	16.7	43.7	17.3	41.7	22.1	49.8
Mus musculus	9.7[k]			4.4	1.3	1.9	0.5	2.9	0.7
Rattus rattus	102.7[k]	6.7	11.5	8.9	27.4	5.8	16.3	7.6	20.0
Primata						5.8	9.7	1.7	2.7
Microcebus tavaratra	61.1[n]					5.8	9.7	1.7	2.7

[a] *Gromphadorhina* sp.
[b] cf. *Laliostoma* sp./*Mantidactylus* spp./*Aglyptodactylus* sp.
[c] cf. *Boophis* sp./*Mantidactylus* spp./*Ptychadena madagascariensis*.
[d] *Mantella* spp./*Anodontohyla* sp./*Cophyla* sp./*Stumpffia* sp.
[e] cf. *Homopholis boivini*/*Uroplatus fimbriatus*/*U. henkeli*.
[f] cf. *Uroplatus sikorae*/*Paroedura homalorhina*/*P. stumpffi*.
[g] cf. *U. ebenaui*/*P. karstophila*/*P. oviceps*/*Geckolepis* spp./*Hemidactylus* spp.
[h] Estimated.
[i] Clarke and Moore (1995).
[j] Estimated (Goodman et al. 1993b).
[k] Goodman et al. (1993b).
[l] SMG, unpubl. data.
[m] Goodman et al. (1991).
[n] Rasoloarison et al. (2000).

madagascariensis, MNI = 1; *Merops superciliosus*, MNI = 1), afrosoricidans and soricomorphans (*Setifer setosus*, MNI = 1; *Suncus madagascariensis*, MNI = 1), rodents (*Mus musculus*, MNI = 8; *Rattus rattus*, MNI = 28), and a northern rufous mouse lemur (*Microcebus tavaratra*, MNI = 1).

DISCUSSION

This work provides new information on the habits of Red Owls in a forest biome in which it was only recently found to occur. Our findings add to knowledge of the distribution, roosting habits, and diet of this rare owl, which has implications for their conservation at Ankarana.

The Ankarana record is the only published account of Red Owls using a cave (Van Esbroek 2006). However, the occurrence of the owl at a different nearby cave suggests it is not an unusual roost site. The continued presence of at least one individual at the site in the dry season of several successive years (1999, 2000, 2001, 2003) suggests the use of

the first site is not incidental. An additional unpublished record of a Red Owl using a cave entrance for roosting elsewhere on the island suggests these owls use caves for roosting more often than previously thought. In 2003, A. Raselimanana and SMG found a single Red Owl roosting in a shallow cave in the Mt. Papango portion of the Parc National de Midongy-Sud (Fig. 1) in an extensive area of humid forest in the southeastern portion of the island. This record is important because it extends the known range of the species to the south (Irwin and Samonds 2002) and shows that it uses caves for roosting in the eastern portion of its range. Use of cave entrances suggests a large number of potential roost sites could be available for Red Owls at Ankarana, a zone of extensive karst, and that Red Owls could occur in other areas with caves or rock crevices. However, Barn Owls appear to use cave entrances more commonly than Red Owls at Ankarana based on our observations.

Our data also expands knowledge of food habits of Red Owls. Early observations suggested this species fed extensively on frogs (Lavauden 1932) and a captive individual fed on frogs (Halleux and Goodman 1994). No anurans occurred in pellets from the Masoala Peninsula (Goodman and Thorstrom 1998). Frogs were present in the Ankarana pellets even though frogs are more abundant on the Masoala Peninsula than at the notably drier Ankarana. Goodman and Thorstrom (1998) found no insects, no *Suncus* spp., and few geckos in pellets from the Masoala Peninsula. We found some insects and many Madagascan pygmy shrews and geckos in pellets from Ankarana. Mean prey weight was lower at Ankarana than on the Masoala Peninsula due to the presence of insects, frogs, and smaller-bodied afrosoricidans in the pellets. The lack of bats or birds, and the importance of tufted-tailed rats and native mammals in the diet of Red Owls remained consistent between Ankarana and Masoala, and appear to distinguish the dietary regime of Red Owls from that of Barn Owls, including at Ankarana, and the Madagascar Owl (*Asio madagascariensis*) on the island (Goodman and Langrand 1993; Goodman and Thorstrom 1998; Goodman et al. 1993a,b; Goodman and Griffiths 2006; Rasoma and Goodman 2007; this study). The absence of birds or bats in the diet of Red Owls is notable given the presence of at least one species of bat in the cave where the owl roosted at Ankarana (Cardiff 2006), and the presence of birds and bats (*Hipposideros commersoni*, *Coleura afra*) (Goodman et al. 2008) in the diet of Barn Owls at Ankarana. Unlike diet, pellet dimensions do not seem to distinguish Red Owls at Ankarana (35–58 × 24–32 mm, $n = 4$) from Barn Owls at other sites on Madagascar (37–62 × 21–33 mm, $n = 23$) (Goodman et al. 1993b) and identification of pellet species origin by size alone is not appropriate.

CONSERVATION IMPLICATIONS

Habitat degradation may threaten Red Owls at Ankarana. This species roosts and feeds in degraded areas on the Masoala Peninsula; the roost at Ankarana is a rocky area surrounded by forest edge not far from degraded forest and savannah. The owls at both sites appear to feed primarily on tufted-tailed rats. Tufted-tailed rats often climb vegetation and trees, do not seem to occur in savannahs, and rarely occur in areas with severely degraded vegetation (Carleton 2003). Ongoing degradation of forests at Ankarana may reduce availability of tsingy tufted-tailed rats as a food source for Red Owls. Forest degradation could also reduce availability of large trees with cavities that remain the only confirmed nest site for this owl (Thorstrom and Rene de Roland 1997), although it is likely that Red Owls nest in rock cavities since it is now known to roost in such cavities.

Additional conservation concerns exist for the Perte des Rivières site at Ankarana. Sediments and debris borne by floodwaters during the wet season, most likely resulting from cyclones and upstream deforestation, have previously blocked most of the length of horizontal cave passage at the roost site (S. G. Cardiff, unpubl. data). The potential effect of blocking of the cave by sediment and debris on the suitability of the site for roosting by Red Owls is unknown. The site is also accessible to tourists and, although descending into the sinkhole is dangerous without proper equipment and expertise, some tourist visits to the bottom occur. Repeated disturbances by tourists or others could possibly cause Red Owls to abandon use of the site. We encourage other studies to examine potential threats

to conservation of Red Owls and interactions between Red Owls and Barn Owls.

ACKNOWLEDGMENTS

We thank the Association National pour la Gestion des Aires Protégées (ANGAP) and the Ministre de l'Environnement, des Eaux et Forêts (MENVEF) for permission to conduct research at Ankarana. We also extend our gratitude to ANGAP Ankarana for support with logistics. This manuscript benefited from comments by several anonymous reviewers. Mohamed, Sabry Mamilaza, and other Ankarana guides initially informed us of the presence of Red Owls and we could not have conducted this study without them. This study is dedicated to the memory of Sabry Mamilaza, who died in 2001. We are also grateful to Lisa Stano, who assisted with collection of owl pellets. We conducted this study under the protocol of collaboration between the Département de Biologie Animale at the Université d'Antananarivo, WWF-Madagascar, and the Field Museum of Natural History. The Volkswagen Foundation and the National Geographic Society (6637-99 and 7402-03) provided funding for inventories in 2001–2003. The U.S. Peace Corps provided support to SGC in 2000–2002. This material is based upon work supported under a National Science Foundation Graduate Research Fellowship to SGC. We thank Russell Thorstrom, Lily Arison Rene de Roland, and Lucienne Wilmé for providing additional information on owl and prey species.

LITERATURE CITED

Cardiff, S. G. 2006. Bat cave selection and conservation in Ankarana, northern Madagascar. Thesis. Columbia University, New York, USA.

Cardiff, S. G. and J. Befourouack. 2003. The Réserve Spéciale d'Ankarana. Pages 1501–1507 *in* The natural history of Madagascar (S. M. Goodman and J. P. Benstead, Editors). University of Chicago Press, Chicago, Illinois, USA.

Carleton, M. D. 2003. *Eliurus*, tufted-tailed rats. Pages 1373–1380 *in* The natural history of Madagascar (S. M. Goodman and J. P. Benstead, Editors). University of Chicago Press, Chicago, Illinois, USA.

Clarke, D. C. and A. J. Moore. 1995. Variation and repeatability of male agonistic hiss characteristics and their relationship to social rank in *Gromphadorhina portentosa*. Animal Behaviour 50:719–729.

Goodman, S. M. and O. Griffiths. 2006. A case of exceptionally high predation levels of *Rousettus madagascariensis* by *Tyto alba* (Aves: Tytonidae) in western Madagascar. Acta Chiropterologica 8: 553–556.

Goodman, S. M. and O. Langrand. 1993. Food habits of the Barn Owl *Tyto alba* and the Madagascar Long-eared Owl *Asio madagascariensis* on Madagascar: adaptation to a changing environment. Musée Royal de l'Afrique Centrale Tervuren, Belgique, Annales Sciences Zoologiques 268:147–153.

Goodman, S. M. and R. Thorstrom. 1998. The diet of the Madagascar Red Owl (*Tyto soumagnei*) on the Masoala Peninsula, Madagascar. Wilson Bulletin 110:417–421.

Goodman, S. M., S. G. Cardiff, and F. H. Ratrimomanarivo. 2008. First record of *Coleura* (Emballonuridae) on Madagascar and identification and diagnosis of members of the genus. Systematics and Biodiversity 6:283–292.

Goodman, S. M., G. K. Creighton, and C. Raxworthy. 1991. The food habits of the Madagascar Long-eared Owl *Asio madagascariensis* in southeastern Madagascar. Bonner zoologische Beiträge 42:21–26.

Goodman, S. M., O. Langrand, and C. J. Raxworthy. 1993a. Food habits of the Madagascar Long-eared Owl *Asio madagascariensis* in two habitats in southern Madagascar. Ostrich 64:79–85.

Goodman, S. M., O. Langrand, and C. J. Raxworthy. 1993b. The food habits of the Barn Owl *Tyto alba* at three sites on Madagascar. Ostrich 64:160–171.

Goodman, S. M., A. Andrianarimisa, L. E. Olson, and V. Soarimalala. 1996. Patterns of elevational distribution of birds and small mammals in the humid forests of Montagne d'Ambre, Madagascar. Ecotropica 2:87–98.

Grandidier, A. 1878. Note sur un nouveau Strigidé de Madagascar. Bulletin de la Société philomathique de Paris 7(2):65–66.

Halleux, D. and S. M. Goodman. 1994. The rediscovery of the Madagascar Red Owl *Tyto soumagnei* (Grandidier 1878) in north-eastern Madagascar. Bird Conservation International 4:305–311.

Hawkins, A. F. A., P. Chapman, J. U. Ganzhorn, Q. C. M. Bloxam, S. C. Barlow, and S. J. Tonge. 1990. Vertebrate conservation in Ankarana Special Reserve, northern Madagascar. Biological Conservation 54:83–110.

Irwin, M. T. and K. E. Samonds. 2002. Range extension of the Madagascar Red Owl *Tyto soumagnei* in Madagascar: the case of a rare, widespread species? Ibis 144:680–683.

International Union for the Conservation of Nature (IUCN). 2006. IUCN Red List of threatened species. International Union for Conservation of Nature and Natural Resources Species Survival Commission, Cambridge, United Kingdom. http://www.iucnredlist.org (accessed 17 May 2006).

Lavauden, M. L. 1932. Etude d'une petite collection d'oiseaux de Madagascar. Bulletin du Muséum national d'Histoire naturelle (2) 4:629–640.

Marti, C. D. 1987. Raptor food habits studies. Pages 67–80 *in* Raptor management techniques manual (B. A. Giron Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird, Editors). National Wildlife Federation, Washington, D.C., USA.

Radofilao, J. 1977. Bilan des explorations spéléologiques dans l'Ankarana. Annales de l'Université de Madagascar, série Sciences de la Nature et Mathématiques 14:195–204.

Rasoloarison, R., S. M. Goodman, and J. U. Gan-

ZHORN. 2000. Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. International Journal of Primatology 21:963–1019.

RASOMA, J. AND S. M. GOODMAN. 2007. Food habits of the Barn Owl (*Tyto alba*) in spiny bush habitat of arid southwestern Madagascar. Journal of Arid Environments 69:537–543.

ROSSI, G. 1976. Karst et dissolution des calcaires en milieu tropical. Zeitschrift für Geomorphologie, Supplementbände 26:124–152.

THORSTROM, R. AND L.-A. RENE DE ROLAND. 1997. First nest record and nesting behaviour of the Madagascar Red Owl *Tyto soumagnei*. Ostrich 68: 42–43.

THORSTROM, R. AND L.-A. RENE DE ROLAND. 2003. *Tyto soumagnei*, Madagascar Red Owl. Pages 1110–1113 *in* The natural history of Madagascar (S. M. Goodman and J. P. Benstead, Editors). University of Chicago Press, Chicago, Illinois, USA.

THORSTROM, R., J. HART, AND R. T. WATSON. 1997. New record, ranging behaviour, vocalization and food of the Madagascar Red Owl *Tyto soumagnei*. Ibis 139:477–481.

VAN ESBROECK, J. 2006. Madagascar Red Owl *Tyto soumagnei* in Ankarana Special Reserve, Madagascar. Bulletin of the African Bird Club 13:205–206.

ZICOMA. 1999. Les Zones d'Importance pour la Conservation des Oiseaux à Madagascar. Projet ZICOMA, Antananarivo, Madagascar.

The Wilson Journal of Ornithology 120(4):897–900, 2008

Bird Responses to a Managed Forested Landscape

Richard H. Yahner[1]

ABSTRACT.—I examined bird population responses to a managed forested landscape resulting from management for Ruffed Grouse (*Bonasus umbellus*) habitat in central Pennsylvania during three consecutive springs, 2005–2007. The number of bird species increased from 2001–2002 (n = 40) to 2005–2007 (n = 46). Abundance of all species combined declined ($0.10 \geq P \geq 0.05$), perhaps because the area was more heterogenous in 2001–2002 than in 2005–2007. Red-eyed Vireo (*Vireo olivaceus*) was the most common species in both 2001–2002 and 2005–2007. Six of the 20 common species were detected only in the treated sector in both periods; none was specific to the reference sector. Despite increased forest maturation, no populations of early successional bird species declined ($P \leq 0.05$) between periods, but populations of three other species did. Management of the Barrens Grouse Habitat Management Area for Ruffed Grouse habitat did not have a profound effect on bird populations from 2001–2002 to 2005–2007 subsequent to the last cutting cycle. *Received 16 January 2008. Accepted 1 May 2008.*

Long-term studies of the responses of birds to managed landscapes are crucial to understanding regional population trends (Gullion 1990; Yahner 2000, 2003). Thus, an important question is not necessarily can habitat be managed for early successional bird species (Yahner 2003), but how soon after management must habitat be manipulated further to ensure adequate early successional habitat is available due to loss via plant succession.

The Barrens Grouse Habitat Management Area (GHMA) was created in 1976 for Ruffed Grouse (*Bonasus umbellus*) habitat via even-aged management (Yahner 1993). Habitat management consisted of the establishment of 4-ha "activity centers" for adult grouse (Gullion 1977), which resulted in a series of 1-ha contiguous plots of different ages in mixed-oak (*Quercus* spp.) and aspen (*Populus* spp.) cover types (Yahner 1993). Grouse habitat management provided valuable breeding habitat for bird species dependent on young forests. The objective of the present study was to compare community structure and composition of breeding birds in the present (2005–2007) 5 years after a fourth cutting cycle (in winters 1999–2000) at the Barrens GHMA to that just after the fourth cycle in 2001–2002) (Yahner 2003).

METHODS

Field work was conducted during three consecutive springs 2005, 2006, and 2007 (late May-mid-Jun) at the Barrens GHMA, which consists of 1,120 ha on State Game Lands

[1] School of Forest Resources, Pennsylvania State University, 119 Forest Resources Building, University Park, PA, 16802, USA; e-mail: rhy@psu.edu

176, Centre County, in the Valley and Ridge Province of Pennsylvania (Yahner 1993) (40° 47′ N, 78° 58′ W). The Barrens GHMA is divided into a treated (managed) sector and a reference (unmanaged) sector of approximately equal area.

The treated sector was 136 contiguous blocks (60 in aspen and 76 in mixed-oak cover type); each block was 4 ha and was subdivided into 1-ha plots (A–D, each ~100 × 100 m) (Yahner 2003). The 60 blocks in aspen cover type were cut in four winter cutting cycles: 1976–77, plot A; 1980–81, plot B; 1986–87, plot C; and 1999–2000, plot D, for a 100% cut. Only plots A–C were cut in the 76 blocks of the mixed-oak type: 1976–77, plot A; 1980–81, plot B; and 1999–2000, plot C, for a 75% cut. Fifteen-20 residual overstory trees (woody stem >7.5 cm dbh, >1.5-m tall) were retained per plot in plots C and D of the aspen type, and in plots B and C of the mixed-oak type.

Overstory trees in the uncut plots (D in mixed oak) of the treated sector and in the reference (unmanaged) sector were ~90–100 years old and consisted mainly of red maple (*Acer rubrum*), white oak (*Quercus alba*), chestnut oak (*Q. montana*), northern red oak (*Q. rubra*), black cherry (*Prunus serotina*), quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidenta*), and pitch pine (*Pinus rigida*) (Yahner 1993, 2003). Major understory trees (woody stem 1–7.5 cm dbh, >1.5-m tall) were red maple, oak, black cherry, and aspen.

I used the same 90 representative plots as in previous studies (Yahner 1993, 1997, 2003). Briefly, 10 plots (A–D) in both cover types of the treated sector (n = 80 plots) and 10 plots in the control sector were selected. Plots were separated by 200 m and plot centers were >50 m from disturbances (e.g., logging roads) to minimize edge effects (Strelke and Dickson 1980, Yahner 1987). Area sampled was 25.4 ha or 2.3% of the total study area.

I visited each plot in late May to early June each year (2005–2007) in a randomized order (Yahner 2003). All birds seen or heard within 30 m of each plot center during a 5-min period after a 1-min equilibrium period were counted. Point counts were made between sunrise and 0900 hrs EST. A 30-m radius point count was used to minimize edge effects at interfaces of plots of different age post-cutting in the treated sector (Repenning and Labisky 1985). Birds flying over a plot were not counted, and movements of individual birds were monitored carefully to reduce the likelihood of counting the same bird more than once in the same morning.

I calculated species richness and total abundance of each species in 2005–2007 combined in each of the three sectors (aspen = 100% clearcut; mixed-oak = 75% clearcut, and reference = 0% clearcut). I compared observed versus expected abundances of all bird species combined and of common species (≥10 contacts in either 2001–2002 or 2005–2007), using Chi-square goodness-of-fit tests (Sokal and Rohlf 1995). I calculated expected number of contacts in 2001–2002 or in 2005–2007 as the total number of contacts observed per period divided by 2 or 3 years, respectively (after Yahner 2003).

RESULTS

The number of species increased from 2001–2002 (n = 40) to 2005–2007 (n = 46) (Table 1). Abundance of all species combined declined ($0.10 \geq P \geq 0.05$) between periods. The most common species in both periods was Red-eyed Vireo (*Vireo olivaceus*). Six of the 20 common species were found only in the treated sector in both periods; none was specific to the reference sector.

Species present on the area in 2001–2002 but not in 2005–2007 were Cooper's Hawk (*Accipiter cooperii*), Ruby-throated Hummingbird (*Archilochus colubris*), Olive-sided Flycatcher (*Contopus cooperi*), Willow Flycatcher (*Empidonax traillii*), and Yellow-breasted Chat (*Icteria virens*). Species absent on the area in 2001–2002 but observed in 2005–2007 were Red-tailed Hawk (*Buteo jamaicensis*), Baltimore Oriole (*Icterus galbula*), Worm-eating Warbler (*Helmitheros vermivorus*), Black-throated Green Warbler (*Dendroica virens*), Blue-winged Warbler (*Vermivora pinus*), Mourning Warbler (*Oporornis philadelphia*), Hooded Warbler (*Wilsonia citrina*), Least Flycatcher (*Empidonax minimus*), Brown Thrasher (*Toxostoma rufum*), Wild Turkey (*Meleagris gallopavo*), and Veery (*Catharus fuscescens*).

Population densities of Gray Catbird (*Du-*

TABLE 1. Population abundance (contacts/100 ha/year) of common species (≥10 contacts during springs (late May–mid-Jun) in either 2001–2002 or 2005–2007) at the Barrens Grouse Habitat Management Area (actual number of contacts in parentheses). Contacts of uncommon species are included in values of species richness and total population abundances of all species combined.

	2001–2002	2005–2007
Blue Jay, *Cyanocitta cristata*[a]	26 (13)	10 (8)
Tufted Titmouse, *Baeolophus bicolor*[b]	10 (5)	22 (17)
Black-capped Chickadee, *Poecile articapillus*	20 (10)	16 (12)
Blue-gray Gnatcatcher, *Polioptila caerulea*	18 (9)	14 (11)
Wood Thrush, *Hylocichla mustelina*[c]	20 (10)	9 (7)
Gray Catbird, *Dumetella carolinensis*[ac]	35 (18)	83 (63)
Eastern Wood-Pewee, *Contopus virens*	14 (7)	13 (10)
Red-eyed Vireo, *Vireo olivaceus*	162 (82)	161 (123)
Chestnut-sided Warbler, *Dendroica pensylvanica*[ac]	32 (16)	92 (70)
Ovenbird, *Seiurus aurocapilla*[a]	122 (62)	69 (53)
Common Yellowthroat, *Geothylpis trichas*[c]	57 (29)	39 (30)
Hooded Warbler, *Wilsonia citrina*[a]	0 (0)	13 (10)
American Redstart, *Setophaga ruticilla*[a]	65 (33)	34 (26)
Rose-breasted Grosbeak, *Pheucticus ludovicianus*	33 (17)	39 (30)
Indigo Bunting, *Passerina cyanea*[c]	39 (20)	33 (25)
Eastern Towhee, *Pipilo erythrophthalmus*	75 (38)	72 (55)
Field Sparrow, *Spizella pusilla*[c]	30 (15)	21 (16)
Chipping Sparrow, *S. passerina*[c]	20 (10)	20 (15)
Scarlet Tanager, *Piranga olivaceus*	30 (15)	28 (21)
Abundance, all species combined[c]	946 (480)	845 (644)
Total number of species	40	46

[a] Population abundance significantly different between periods ($\chi^2 \geq 3.84$, df = 1, $P \leq 0.05$).

[b] Population abundance slightly different between periods ($\chi^2 \geq 2.71$, df = 1, $0.10 \geq P \geq 0.05$).

[c] Species observed only in the treated sector.

metella carolinensis), Chestnut-sided Warbler (*Dendroica pensylvanica*), and Hooded Warbler dramatically increased ($P \leq 0.05$) from 2001–2002 to 2005–2007 at the Barrens GHMA (Table 1). Populations of Tufted Titmice (*Baeolophus bicolor*) also had significant increases ($0.10 \geq P \geq 0.05$) from 2001–2002 to 2005–2007. No populations of early successional bird species declined ($P \geq 0.05$) over time despite increased forest maturation from 2001–2002 to 2005–2007. Populations of three species declined ($P \leq 0.05$) from 2001–2002 to 2005–2007: a woodland species, Ovenbird (*Seiurus aurocapilla*), a secondary forest species, American Redstart (*Setophaga ruticilla*), and a corvid, Blue Jay (*Cyanocitta cristata*).

DISCUSSION

I attributed a higher number of species in 2005–2007 on the Barrens GHMA, in part, to different levels of sampling between periods (e.g., 2 vs. 3 consecutive years, respectively). Perhaps the decline in abundance of all species combined was a result of the site being more heterogeneous in 2001–2002 than in 2005–2007.

Populations of Blue-winged Warbler may be increasing in central Pennsylvania at the expense of populations of Golden-winged Warbler (*Vermivora chrysoptera*) (Kubel 2005), but the Blue-winged Warbler was absent earlier on the area (Yahner 1997, 2003).

Population declines of Ovenbird at the Barrens GHMA in 2005–2007 paralleled significant Pennsylvania decreases in populations of this species according to the Breeding Bird Survey (BBS) (USDI 2007) during the period from 1980 to 2006. According to the BBS, American Redstart and Blue Jay populations in Pennsylvania have not declined significantly during this period. Blue Jays, however, may be experiencing localized population decreases due to West Nile virus (Male 2003, Rohnke 2005).

Gray Catbird populations increased in 2005–2007, but no similar trend was found in BBS data for Pennsylvania (USDI 2007). In contrast, populations of both Chestnut-sided and Hooded warblers increased significantly based on BBS data for Pennsylvania. I suspect that increases in populations on the area of these latter two species were due to regional

trends and were affected positively by presence of older habitat, especially in aspen D and in oak C plots on my study site. Chestnut-sided Warblers were especially abundant in these types of plots at the Barrens GHMA (Schill 2007).

My prediction (Yahner 2003) that early successional species would decline in 2005–2007 did not occur at the Barrens GHMA. It is probable that plant succession has not progressed adequately to affect population densities of these species, despite 5–7 years having elapsed since the last cutting cycle on the area. Populations of Field Sparrows (*Spizella pusilla*) were quite low at the Barrens GHMA prior to the fourth cutting cycle in 1999–2000; subsequent to this cycle, populations increased significantly (Yahner 2003) and have not changed since, based on results obtained in the present study. Habitat management for Ruffed Grouse on the Barrens GHMA generally did not have a profound effect on the sympatric bird community after the last cutting cycle. It is probable that more time must elapse before significant responses by bird populations will occur as a result of even-aged management at the Barrens GHMA.

ACKNOWLEDGMENTS

This study was funded by the Pennsylvania Agricultural Experiment Station. I thank H. L. Besecker for clerical assistance.

LITERATURE CITED

Gullion, G. W. 1977. Forest manipulation for Ruffed Grouse. Transactions of the North American Wildlife and Natural Resources Conference 42:449–458.

Gullion, G. W. 1990. Forest-wildlife interactions. Pages 349–383 *in* Introduction to forest science (R. A. Young and R. L. Griese, Editors). Second Edition. John Wiley and Sons, New York, USA.

Kubel, J. E. 2005. Breeding ecology of Golden-winged Warblers in managed habitats in central Pennsylvania. Thesis. Pennsylvania State University, University Park, USA.

Male, T. 2003. Potential impact of West Nile virus on American avifaunas. Conservation Biology 17: 928–930.

Repenning, R. W. and R. F. Labisky. 1985. Effects of even-age management on bird communities of the longleaf pine forest in northern Florida. Journal of Wildlife Management 49:1088–1098.

Rohnke, A. T. 2005. Possible ecological effects of habitat alteration and West Nile virus on songbird populations in central Pennsylvania. Thesis. Pennsylvania State University, University Park, USA.

Schill, K. L. 2007. Habitat use and nesting ecology of Chestnut-sided Warblers. Thesis. Pennsylvania State University, University Park, USA.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry. Third Edition. W. H. Freeman and Company, New York, USA.

Strelke, W. K. and J. G. Dickson. 1980. Effect of forest clear-cut edge on breeding birds in east Texas. Journal of Wildlife Management 44:559–567.

U. S. Department of Interior (USDI). 2007. Breeding Bird Surveys. USDI, Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.pwrc.usgs.gov/BBS/ (accessed 20 December 2007).

Yahner, R. H. 1987. Use of even-aged stands by winter and spring bird communities. Wilson Bulletin 99:218–232.

Yahner, R. H. 1993. Effects of long-term forest clear-cutting on wintering and breeding birds. Wilson Bulletin 105:239–255.

Yahner, R. H. 1997. Long-term dynamics of bird communities in a managed forested landscape. Wilson Bulletin 109:595–613.

Yahner, R. H. 2000. Long-term effects of even-aged management on bird communities in central Pennsylvania. Wildlife Society Bulletin 28:1102–1110.

Yahner, R. H. 2003. Responses of bird communities to early successional habitat in a managed landscape. Wilson Bulletin 115:292–298.

The Wilson Journal of Ornithology 120(4):901–905, 2008

Freeze-Frame Fruit Selection by Birds

Mercedes S. Foster[1]

ABSTRACT.—The choice of fruits by an avian frugivore is affected by choices it makes at multiple hierarchical levels (e.g., species of fruit, individual tree, individual fruit). Factors that influence those choices vary among levels in the hierarchy and include characteristics of the environment, the tree, and the fruit itself. Feeding experiments with wild-caught birds were conducted at El Tirol, Departamento de Itapúa, Paraguay to test whether birds were selecting among individual fruits based on fruit size. Feeding on larger fruits, which have proportionally more pulp, is generally more efficient than feeding on small fruits. In trials (n = 56) with seven species of birds in four families, birds selected larger fruits 86% of the time. However, in only six instances were size differences significant, which is likely a reflection of small sample sizes. *Received 15 August 2007. Accepted 26 February 2008.*

Frugivorous birds have the potential to choose among food items at multiple hierarchical levels (Sallabanks 1993, Wheelwright 1993). They can choose among different species of fruits, among individual trees of a preferred species of fruit, and among individual fruits on their chosen tree. Once a fruit is plucked and perhaps 'tested' in the bill, a bird can choose to discard the fruit or continue to feed on it. Factors influencing choice may be external to the plant, characteristics of the plant unrelated to the fruit, or characteristics of the fruit. External factors include nature of the habitat and presence nearby of fruiting individuals of the same or other species (e.g., Foster 1990, Saracco et al. 2005). Relevant characteristics of the plant include crown size, foliage density,. and fruit abundance (Foster 1990, Sallabanks 1992, Laska and Stiles 1994, Ortiz-Pulido and Rico-Gray 2000). Characters of fruits can be either extrinsic (e.g., accessibility, Moermond and Denslow 1983, Levey and Moermond 1984) or intrinsic (e.g., pulp: seed ratio, nutrient content, amount of pulp, fruit and seed size, parasite infestation, color, taste, ripeness, etc.). Potentially, characters in all these categories can influence choice of a fruit species or of an individual tree in which to feed; only a subset of the characters can influence the selection of a particular fruit and the decision to eat it or not.

Considerable effort has been invested in examining the basis of choice at all levels, and nearly every external, tree, and fruit feature has been correlated with species preference, visitor frequency, or fruit removal rate in one plant species or another (e.g., Sorenson 1983, 1984; Johnson et al. 1985; Piper 1986; Hedge et al. 1991; White and Stiles 1991; Sallabanks 1992, 1993; Willson and Comet 1993; Willson and Whelan 1993; Whelan and Willson 1994; Stanley and Lill 2002; Stanley et al. 2002). However, clear patterns of correlations have not emerged, although visitor frequency, absolute number of fruits removed, and proportion of fruits removed are often correlated with size of the initial fruit crop (e.g., Foster 1990, Laska and Stiles 1994, Ortiz-Pulido and Rico-Gray 2000). The absence of strong, widespread correlations between visitation rates and fruit characteristics is counter intuitive. Frugivores should maximize their feeding efficiencies (benefit obtained from the fruit/cost of fruit handling) among conspecific plants by preferentially feeding in trees with the largest or most nutritious fruits to maximize benefits; trees whose fruits have the smallest seeds (ballast) to minimize costs; or trees whose fruits have the greatest pulp:seed ratio (e.g., Martin 1985, Wheelwright 1993). The absence of a correlation between rate of fruit removal and any fruit trait could reflect the variability of those traits among fruits within trees and the hierarchical nature of the points of choice. A bird could use a non-fruit criterion (e.g., foliage density or fruit abundance) to select a tree for feeding and then use a fruit character to select among the fruits in that tree based on traits that maximize feeding efficiency.

[1] USGS, Patuxent Wildlife Research Center, National Museum of Natural History, P. O. Box 37012, Washington, D.C. 20013, USA; e-mail: fosterm@si.edu

I examined this possibility in Cocú (*Allophylus edulis*, Sapindaceae), whose fruits (6.7–9.4 × 6.6–9.6 mm) are eaten by at least 26 species of birds (Foster 1987). The birds feed with noticeably different frequencies in individual Cocú trees (Foster 1990). The only tree/fruit characteristic with which visitation rates are broadly correlated is size of the fruit crop. Abundance of fruits is highly correlated with tree crown size and foliage density, which may be the operant characteristics. General correlations with fruit characteristics have not been noted (Foster 1990). The only *Allophylus* fruit characteristics visually available to birds are color, size, and shape although birds that manipulate the fruit with the bill may be able to detect pulp:seed ratio and/or seed size or larval infestation. Taste or smell may allow birds to detect nutrient content or presence of toxic substances (Sorenson 1983). I have no knowledge of either of the latter possibilities for *A. edulis* and focused on visual cues. Birds ate only obviously ripe fruits of *A. edulis* in 216 hrs of observation. Ripe fruits are a uniform bright, shiny red, and shape is equally uniform. Therefore, I only considered fruit size. The objectives of the study were to: (1) establish which fruit characters with a potential to influence feeding efficiency directly (i.e., amount of pulp, size of seed, pulp:seed ratio) were correlated with fruit size, and (2) conduct cage experiments to investigate whether birds were choosing fruits on the basis of size.

METHODS

Allophylus edulis occurs in southern South America east of the Andes (Lopez et al. 1987). I studied it in the vicinity of El Tirol (27° 11′ S, 55° 46.5′ W), ~19.5 km by road NNE of Encarnación, Departamento de Itapúa, Paraguay, in a remnant of Atlantic Forest. The area is described in Smith and Foster (1984). Tree and bird characteristics, and interactions have been reported elsewhere (Foster 1987, 1990).

I examined pulp weight/fruit, seed weight/fruit, and pulp:seed ratio with random samples of fruits (n = 10–31) from 14 trees (6 trees in 1981 and 1983, plus 2 additional trees in 1983) to see if they were correlated with fruit size. Because *Allophylus* fruits are spherical with somewhat flattened ends, I calculated size as the volume (mm^3) of a cylinder ($V = \pi r^2 h$; r = radius, h = height), even though differences between fruit height and diameter rarely exceeded 1 mm and were all <5 mm. Whole fruits were weighed to 0.01 g on a field balance; seeds were removed from the fruits, cleaned, and weighed; and pulp weight was calculated by subtraction. These values were used to calculate the pulp:seed ratio. I have no data on the nutrient and energy contents of individual fruits although composite samples from individual trees often differed (Foster 1990). However, increased pulp at any size translates to an absolute increase in energy and nutrients.

Birds known to eat Cocú were mist-netted in the forest in 1978 and 1980–1982, placed in inverted mosquito head nets (28 × 38 cm) with wire frames that kept them open and a stick perch, and taken to the test area. Birds were held 1–2 hrs in the dark prior to testing and then introduced into a cage (100 × 75 × 100 cm high) of gray fiberglass screen with one lengthwise and one crosswise horizontal perch.

I introduced 20 freshly collected and measured (height and diameter with calipers) fruits into the cage once a bird was accustomed to it and had rested calmly for 15 min. Each fruit was hooked to the tip of a fine wire attached to a frame of 2-mm-diameter dowels suspended from the roof of the cage. Ten fruits were positioned on either side of and parallel to but above the lengthwise perch with distances from the perch depending on the size of the bird. Birds were able to reach and pluck a fruit but also could move freely along the perch without touching the fruits. Fruit positions were numbered consecutively. Fruits were selected to cover a large range of sizes (volumes) and randomly attached to the wires. The volume of the fruit at each position was recorded. I recorded the position number of each fruit from a blind (~2 m distant) as it was eaten. I terminated a trial after a bird had eaten about half the fruits, had not fed after 30 min in the cage, or if an initial period of feeding was followed by a 15-min period of non-feeding. Each bird was held in the head net for 1–2 hrs at the end of its first trial and then used for a second trial. The right outer tail feather of each test bird was clipped so that it could be recognized if netted subse-

TABLE 1. Average sizes of fruits eaten (E) or not eaten (NE) in fruit selection trials, by bird species.

Species	Trials *n*	Differences in $\bar{X}$ fruit sizes (E − NE), all trials		Birds *n*	Differences in $\bar{X}$ fruit sizes (E − NE), all birds[a]	
		mm^3	*P*[b]		mm^3	*P*[b]
Blue Manakin (*Chiroxiphia caudata*)	5	17	0.320	3	12	0.612
Pale-breasted Thrush (*Turdus leucomelas*)	4	(12)[c]	0.688	2	(52)[c]	0.549
Black-goggled Tanager (*Trichothraupis melanops*)	23	31	0.003	13	33	0.016
Ruby-crowned Tanager (*Tachyphonus coronatus*)	11	39	0.006	6	28	0.157
Violaceous Euphonia (*Euphonia violacea*)	6	63	<0.001	3	44	0.101
Guira Tanager (*Hemithraupis guira*)	5	35	0.059	4	40	0.030
Red Pileated Finch (*Coryphospingus cucullatus*)	2	39	0.214	1	42	0.478
All species combined	56	31	<0.001	32	28	0.001
	512/608[d]			271/368[d]		

[a] Only the first trial is included for birds with two trials.
[b] *P* = probability (*t* test) that average sizes (mm^3) of eaten and not eaten fruits are equal.
[c] Parentheses = average size of fruits not eaten > average size of fruits eaten.
[d] Total fruits at 20/trial, E/NE.

quently; no bird was used for more than two trials.

I tested the significance of correlations between fruit size and other fruit characteristics with linear regression analysis. To learn if individual birds were discriminating among available fruits by size, I compared the average volume of fruits selected in each trial with that of the fruits that were not selected. I also compared the combined data for all trials for each species as well as the combined data for all trials of all species. Finally, I repeated the latter two comparisons including data from only a single trial (the first) for each bird, even though the 1–2-hr period that elapsed between trials was likely sufficient to make them independent. I tested for homogeneity of variances (*F* test) and compared means with either a two-sample Student's *t*-test (equal variances) or Welch's *t*-test (unequal variances). I used a sign test to examine if differences between average volumes of eaten and uneaten fruits in each trial were in the same direction, i.e., if eaten fruits were the larger, even if differences were not significant. I used PAST Version 1.78 (Hammer et al. 2001) for all analyses.

RESULTS

Pulp weight per fruit was positively correlated (r values = 0.6915–0.9814; all $P < 0.002$) with fruit volume in all 14 samples. Results for both seed weight and pulp:seed ratio were mixed. Both traits were positively correlated with fruit volume, but only six of the seed weight correlations were significant (r = 0.3591–0.8845; P = 0.0001–0.047) and only seven of the pulp:seed ratio correlations (r = 0.5785–0.8027; P = 0.001–0.024). The slopes of the relationships of pulp weight, seed weight, and pulp:seed ratio to fruit volume were 0.0013X, 0.0006X, and 0.009X, respectively.

Thirty-two individuals of seven species in four families selected and ate fruits in 56 trials (Table 1). Some birds plucked fruits while on a main perch; others removed them by hover-plucking or perching on the wooden fruit display frame and reaching downward. The average volumes of the eaten and uneaten fruits differed in 55 of 56 trials; the eaten fruits were larger (sign test, r = 48, $P \leq 0.001$) more often (n = 48) than were uneaten fruits (n = 7). However, in only six (11%) of all trials, spread among five bird species, were differences in average volumes of the eaten and uneaten fruits significant, likely because of small sample sizes (20 fruits/trial); in each case the fruits selected by birds were larger than those not selected. Average volumes of eaten and uneaten fruits differed significantly when values for all tests were combined (Table 1). The same was true when only a single trial was included for each bird. In the comparisons by species, size differences were significant only for Black-goggled Tanager, Ruby-crowned Tanager, and Violaceous Euphonia (scientific names are in Table 1), although α was 0.059 for Guira Tanager. Differences were significant for all species combined and Black-goggled and Guira tanagers when tests were con-

ducted using only a single sample for each bird (Table 1).

DISCUSSION

Frugivorous birds are particularly suited for studies of foraging and feeding behavior because locations of their feeding areas (fruiting plants) are fixed and their 'prey items' (fruits) do not attempt to escape. Thus, feeding sites used and fruits eaten generally represent choice rather than opportunistic consumption of a suitable food item that serendipitously appears. I hypothesized that birds feeding on *A. edulis* would select the largest fruits available, a practice that has been demonstrated previously in other bird species (e.g., Johnson et al. 1985, Piper 1986, White and Stiles 1991, Sallabanks 1993, Wheelwright 1993, Stanley et al. 2002). Seed size (ballast) increases with increasing fruit size, but amount of pulp increases at a faster rate. Consequently, larger fruits supply greater amounts of pulp and have a greater pulp:seed ratio. Both of these conditions enhance feeding efficiency, especially among Type III (push and bite) feeders (e.g., *Euphonia* spp., Foster 1987). Birds in cage tests generally (86% of the trials and 86% of the species) selected fruits that were larger than those not selected, regardless of feeding type. The lack of significance among the differences likely reflects the small sample sizes. The probability that sizes of eaten and uneaten fruits were statistically the same, in most instances, increased when n decreased, when only a single trial for each bird was included in the analysis. The seeming anomalous result from the Pale-breasted Thrush in which uneaten fruits averaged larger than those eaten (although not significantly) likely reflects small sample size.

Birds selected larger fruits on average, even though differences were only occasionally statistically significant. This may reflect a 'freeze-frame' foraging strategy in which a bird selects a fruit only from among those within its immediate field of vision, where sizes can be directly compared. In this scenario, the bird selects one of the larger fruits within the frame even though the frame does not necessarily include the largest fruits on the tree or even any fruits in the upper half of the size range of fruits on the tree. After eating 1–2 fruits, the bird changes perches and views the fruits in another frame.

Martin (1985) suggested that birds should prefer fruits that are within an optimal size range defined by handling time (including search time) and reward size. Handling costs also increase as fruit size increases until they outweigh the benefits derived from eating a larger fruit. The increased search time required to review and compare sizes of some proportion of fruits before selecting one on a tree such as Cocú could increase costs beyond the increase in benefits from selecting a larger fruit. The cost increase might be even greater if ascertaining the direction of size differences among separated fruits and retaining the locations of previously viewed fruits were difficult, and required moving between fruits more than once. Avery et al. (1993) demonstrated for Cedar Waxwings (*Bombycilla cedrorum*) that average diameters of test fruits had to differ by some threshold amount before the birds exhibited size preferences, and that birds did not exhibit a preference between fruits of adjacent size classes. Their work suggested that birds were less able to recognize threshold differences when fruit sizes, rather than comprising discrete categories, formed a continuum as in *Allophylus*. As long as fruit sizes are within the optimal size range for the species, the increased time required by a bird to compare a large sample of fruits before selecting one might reduce the extra benefits from feeding on larger fruits to insignificance. This could be particularly applicable when numbers of fruits that birds must eat to meet daily existence energy needs are small and feeding time minimal, as with *Allophylus*, especially for Type I (pluck and swallow) and Type II (cut or mash) feeders (Foster 1987). Increased activity in the tree might also attract predators and increase vulnerability of the birds.

Birds appear to exert choice at two levels when feeding on *Allophylus edulis* fruits, first by selecting a feeding tree based on fruit abundance and second by selecting among fruits within that tree based on size. Testing to learn if they accomplish the latter by freeze-frame foraging will require additional cage experiments and observations of feeding birds in the wild, using a variety of plant species whose fruits differ in size.

ACKNOWLEDGMENTS

I thank the Paraguayan Ministry of Agriculture, Hernando Bertoni, and Hilario Moreno for facilitating research permits; Miguela and Armando Reynaers for permission to work at El Tirol, hospitality, and logistic support; E. W. Schupp for assistance in the field; and S. W. Droege and L.-A. Hayek for advice on statistical analyses. S. W. Droege, D. C. Hahn, and two anonymous reviewers provided useful comments on an early draft of the manuscript. Financial support for field work was provided by the Museum of Vertebrate Zoology, University of California, Berkeley, and the U. S. Fish and Wildlife Service.

LITERATURE CITED

Avery, M. L., K. J. Goocher, and M. A. Cone. 1993. Handling efficiency and berry size preferences of Cedar Waxwings. Wilson Bulletin 105:604–611.

Foster, M. S. 1987. Feeding methods and efficiencies of selected frugivorous birds. Condor 89:566–580.

Foster, M. S. 1990. Factors influencing bird foraging preferences among conspecific fruit trees. Condor 92:844–854.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1):1–9.

Hedge, S. G., K. N. Ganeshaiah, and R. U. Shaanker. 1991. Fruit preference criteria by avian frugivores: their implication for the evolution of clutch size in *Solanum pubescens*. Oikos 60:20–26.

Johnson, R. A., M. F. Willson, J. N. Thompson, and R. I. Bertin. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66:819–827.

Laska, M. S. and E. W. Stiles. 1994. Effects of crop size on intensity of fruit removal in *Viburnum prunifolium* (Caprifoliaceae). Oikos 69:199–202.

Levey, D. J. and T. C. Moermond. 1984. Fruit choice in neotropical birds: the effect of distance between fruits on preference patterns. Ecology 65:844–850.

Lopez, J. A., E. L. Little Jr., G. F. Ritz, J. S. Rombold, and W. J. Hahn. 1987. Arboles Comunes del Paraguay. Peace Corps, Washington, D.C., USA.

Martin, T. E. 1985. Resource selection by tropical frugivorous birds: integrating multiple interactions. Oecologia 66:553–573.

Moermond, T. C. and J. S. Denslow. 1983. Fruit choice in neotropical birds: effects of fruit type and accessibility on selectivity. Journal of Animal Ecology 52:407–419.

Ortiz-Pulido, R. and V. Rico-Gray. 2000. The effect of spatio-temporal variation in understanding the fruit crop size hypothesis. Oikos 91:523–527.

Piper, J. K. 1986. Seasonality of fruit characters and seed removal by birds. Oikos 46:303–310.

Sallabanks, R. 1992. Fruit fate, frugivory, and fruit characteristics: a study of the hawthorn, *Crategus monogyna* (Rosaceae). Oecologia 1992:296–304.

Sallabanks, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. Ecology 74: 1326–1336.

Saracco, J. F., J. A. Collazo, M. J. Groom, and T. A. Carlo. 2005. Crop size and fruit neighborhood effects on bird visitation to fruiting *Schefflera morototoni* trees in Puerto Rico. Biotropica 37:81–87.

Smith, A. R. and M. S. Foster. 1984. Chromosome numbers and ecological observations of ferns from El Tirol, Paraguay. Fern Gazette 12:321–329.

Sorensen, A. E. 1983. Taste aversion and frugivore preference. Oecologia 56:117–120.

Sorensen, A. E. 1984. Nutrition, energy and passage time: experiments with fruit preference in European Blackbirds (*Turdus merula*). Journal of Animal Ecology 53:545–557.

Stanley, M. C. and A. Lill. 2002. Importance of seed ingestion to an avian frugivore: an experimental approach to fruit choice based on seed load. Auk 119:175–184.

Stanley, M. C., E. Smallwood, and A. Lill. 2002. The response of captive Silvereyes (*Zosterops lateralis*) to the colour and size of fruit. Australian Journal of Zoology 50:205–213.

Wheelwright, N. T. 1993. Fruit size in a tropical tree species: variation, preference by birds, and heritability. Vegetatio 107/108:163–174.

Whelan, C. J. and M. F. Willson. 1994. Fruit choice in migrating North American birds: field and aviary experiments. Oikos 71:137–151.

White, D. W. and E. W. Stiles. 1991. Fruit harvesting by American Robins: influence of fruit size. Wilson Bulletin 103:690–692.

Willson, M. F. and T. A. Comet. 1993. Food choices by Northwestern Crows: experiments with captive, free ranging and hand-raised birds. Condor 95:596–615.

Willson, M. F. and C. J. Whelan. 1993. Variation of dispersal phenology in a bird-dispersed shrub, *Cornus drummondii*. Ecological Monographs 63: 151–172.

The Wilson Journal of Ornithology 120(4):906–910, 2008

Predation of Rio Grande Wild Turkey Nests on the Edwards Plateau, Texas

Justin Z. Dreibelbis,[1] Kyle B. Melton,[2] Ray Aguirre,[3] Bret A. Collier,[1,5] Jason Hardin,[4] Nova J. Silvy,[1] and Markus J. Peterson[1]

ABSTRACT.—We followed the fate of nests of Rio Grande Wild Turkeys (*Meleagris gallopavo intermedia*) on the Edwards Plateau of Texas during 2006 and 2007 using motion-activated digital cameras on a subset of nests to evaluate the frequency of nest predation and to identify nest predators. Predation was the primary cause of loss for nests with cameras, accounting for 57 and 65% in 2006 and 2007, respectively. Predation for nests without cameras also was high (69 and 65% for 2006 and 2007, respectively) suggesting the cameras did not increase the probability of nest failure. We documented partial-and multiple-predator events that could result in misidentification of nest predators. Our results provide insight into nest predator communities and confirm that multiple predator events occur with regularity in the wild. *Received 3 December 2007. Accepted 29 April 2008.*

Natality is one of the primary biological processes influencing dynamics of wildlife populations (Everett et al. 1980). Understanding which factors cause changes in individual and group natality is important for managing bird populations. Methods to estimate and understand components of nest survival have received recent attention, particularly for species of ground nesting birds (Dinsmore et al. 2002, Shaffer 2004, Grant et al. 2005). A variety of factors can influence nest survival, but for ground nesting birds, nest predation appears most influential (Ricklefs 1969, Farnsworth and Simons 2000, Rollins and Carroll 2001, Stephens et al. 2005). Given the vulnerability of ground nesting species, predation will affect nest survival and population productivity (Baker 1978, Rollins and Carroll 2001).

Accurate identification of nest predators of ground nesting birds is important in understanding effects of predation on population parameters (Lariviere 1999, Rader et al. 2007). Nest predation studies often rely on physical evidence at the nest, such as tracks, hair, and eggshell fragments to identify predators (Major 1991, Lariviere 1999). Use of physical evidence can be highly subjective (Trevor et al. 1991, Lariviere 1999), and may fail to account for multiple-predator and partial-predation events (Leimgruber et al. 1994). Predation events may be difficult to identify if eggshells are removed by the incubating hen following partial nest predation (Lariviere and Walton 1998), or if predation is by reptilian or avian species, as snakes consume whole eggs in the nest (Staller 2001) and avian species often remove eggs from the nest before consumption (Montevecchi 1976).

Abundance of Rio Grande Wild Turkeys (*Meleagris gallopavo intermedia*) on the southeastern Edwards Plateau, Texas has declined since the late 1970s (Randel et al. 2005, Collier et al. 2007a). Recent work has focused on evaluating factors contributing to this decline (Collier et al. 2007b), including variation in reproductive potential and nest survival (Melton 2007). Predation is the primary cause of nest failure in the region (Cook 1972, Melton 2007), and nest loss can adversely influence Wild Turkey populations (Davis 1959, Baker 1978). Our objectives were to: (1) identify predators of Rio Grande Wild Turkey nests and (2) examine the frequency of total nest loss, partial predation events, and multiple-predator predation events.

METHODS

Study Area.—Our study area was within the Edwards Plateau region of Texas; we studied

[1] Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA.

[2] Texas Parks and Wildlife Department, Waco, TX 76706, USA.

[3] Texas Parks and Wildlife Department, Comfort, TX 78013, USA.

[4] Texas Parks and Wildlife Department, Palestine, TX 75803, USA.

[5] Corresponding author; e-mail: bret@tamu.edu

Wild Turkey nesting from January through July 2006 and 2007 on four sites in Kerr, Real, Bandera, and Medina counties. All study sites were rangelands with flat to rolling divides, shallow soils, and limestone bedrock (Gould 1975), and included private ranches and the Kerr Wildlife Management Area (Texas Parks and Wildlife Department). Study sites ranged in size from 984 to 8,858 ha and all were managed for hunting of native and exotic wildlife; livestock grazing occurred on three of the sites (Kerr, Medina, and Bandera counties).

Field Procedures.—We trapped Wild Turkey hens during January–March, 2006 and 2007. We attached radio transmitters (69.0–95.0 g; Advanced Telemetry Systems, Isanti, MN, USA) to 39 and 22 hens in 2006 and 2007. We located individual hens three times weekly (White and Garrott 1990) during the breeding season until behaviors indicated a hen had initiated a nest (Ransom et al. 1987). We located nests within 1 day after we suspected hens had begun incubation. Once located, we ascertained initiation date, clutch size, and approximate age for each nest. We estimated nest age and initiation date by backdating from the day we found the nest to the day we first located the hen in the nest area. We defined the active nesting period as 39 days; the sum of the average number of eggs in a clutch (11) and a 28-day incubation period (Bailey and Rinnell 1967, Melton 2007). We floated eggs to estimate age of nests found during incubation (Westerskov 1950), and monitored nests three times weekly from a distance of ≥100 m to prevent further disturbance to the hen. We assumed the nest was active if hen locations remained constant. One week before estimated hatch date, we visited nests daily to ensure accurate identification of hatch date.

We used motion-activated trail cameras (Game Spy 100 and Outfitter Cam, Moultrie Feeders, Alabaster, AL, USA) at a sample of nests. Each camera was equipped with 16 MB of internal memory (we added a 256 MB memory card to each camera in 2007), a 10.2 mm lens, and a 9.14 m flash. We learned through a pilot study in 2005 that cameras set within 5 m of a nest require flash reduction, otherwise night photographs were over-exposed. To reduce flash, we covered 100% of the flash surface with one to three layers of masking tape, dependent upon nest distance (most often one layer/m from the nest under 5 m). We attached the camera, based on vegetation surrounding the nest area, to a tree near the nest or to a post. We programmed cameras to take two pictures ~5 sec apart, followed by a 5 or 10-min delay. After the delay period, the next event in the nest area would trigger the camera. We checked cameras after initial setup, only when the bird was located out of the nesting area for more than 1 day. Nests receiving camera surveillance were chosen randomly across study sites depending on camera availability and nest initiation timing.

TABLE 1. Nest predators documented via remotely–triggered cameras at active Rio Grande Wild Turkey nests in the Edwards Plateau, Texas, 2006–2007 (n = number of nests with photographed predation events).

Species	2006 (n = 7 nests)	2007 (n = 11 nests)
Nine-banded armadillo (*Dasypus novemcinctus*)	0	1
Bobcat (*Lynx rufus*)	0	1
Feral hog (*Sus scrofa*)	2	1
Gray fox (*Urocyon cinereoargenteus*)	4	2
Common raccoon (*Procyon lotor*)	2	7
Common Raven (*Corvus corax*)	0	3
Striped skunk (*Mephitis mephitis*)	2	0
Texas rat snake (*Elaphe obsolete lindheimeri*)	1	0
Total multiple predator events	3	4

RESULTS

We placed cameras at 21 of 47 active turkey nests in 2006, with 12 (57%) nests depredated and eight (38%) nests abandoned. These rates are comparable to 69% depredation and 15% abandonment for those nests in our study without cameras. Three of 12 depredated nests with cameras involved more than one predator, four involved a single predator, and five had no photographs of the nest predator (Table 1). We placed cameras at 31 of 71 active nests in 2007. Twenty of 31 (65%) nests with cameras were depredated and 6 of 31 (19%) were abandoned. Four of the depredated nests in-

volved more than one predator, seven involved a single predator, and nine had no predator photographs. We observed 68% (27/40) predation and 18% (7/40) abandonment at nests without cameras in 2007. Nests survived on average 12.5 and 13.0 days with and without cameras in 2006, and 18.4 and 18.7 days with and without cameras in 2007.

We were able to examine timing of predation events in greater detail on approximately half the nests with cameras. For example, a multiple predator event occurred at a nest of a yearling hen found incubating her first nest containing 11 eggs on 17 May 2006. We flushed the hen, estimated nest age at 6 days of incubation, and placed a camera at the nest. We recorded a remarkable series of predation events on 19 May at this nest. At 1818 hrs, a common raccoon (scientific names of predator species are in Table 1) was recorded leaving the nest area and subsequent photographs showed a raccoon consuming an egg ~2 m from the nest. Later that evening (2212 hrs), two photographs (<10 sec apart) were taken of a raccoon predating the nest. Shortly thereafter (2242 hrs), a gray fox visited the nest. Less than 1 hr later (2328 hrs), a striped skunk depredated the nest followed by a gray fox that visited the nest at 2344 hrs. We documented additional predator visits on subsequent days. Raccoons were observed at the nest on 20 May at both 0111 and 0705 hrs as well as on 22 May at 0005 hrs. We photographed feral hogs at the nest on 22 May at 0534 hrs and 2315 hrs, removing the remaining shell fragments from earlier predation events. The last recorded nest visitor was a raccoon on 24 May at 0409 hrs. The hen remained in the general vicinity of the nest until 24 May when we examined the nest site at 1126 hrs, finding no eggshell remains and little disturbance to the leaf litter. Given there was no evidence (egg shells, tracks, scat, hair, etc.) at the nest site when researchers arrived, we initially believed a reptilian or avian predator was responsible.

We also documented an instance of partial nest predation. We located the nest on 17 April 2006, during incubation by an adult hen of her first nest of the season, which contained 16 eggs. We monitored the nest for 28 days, which was successful, and located the hen with eight poults on 14 May. When we returned to the nest area to collect eggshells, we found remnants of only nine hatched eggs. Upon checking the photographs, we found the nest had been partially depredated by a Texas rat snake 11 days earlier. On 3 May at 2118 hrs, we photographed the snake in the nest. The hen hatched the remaining nine eggs on 13 May 2006. There was no physical evidence at the nest, and we initially believed the nest was predated by either a reptilian or avian predator.

DISCUSSION

Our observations indicate that nest predation was the proximate factor affecting overall nest survival of Rio Grande Wild Turkeys during our study, although our sample of nests was fairly small. Additionally, our results suggest that nest predation events involving multiple predators were common. There is a diverse predator community on the Edwards Plateau (Davis and Schmidly 1994) and key predators can change from year to year. The method of depredation used and the evidence left at the nest site after depredation events (e.g., eggshell fragments) may overlap among species. Gray fox were documented in 2006 at 57% of the predation events but were photographed at only 2 (18%) predation events in 2007 (both of which involved multiple predators). Three of 11 (27%) camera nests in 2007 identified Common Ravens removing eggs; however, no ravens were photographed in 2006. Nests depredated by ravens were similar to those depredated by snakes as they contained no shell fragments and had little disturbance around the nest.

Staller (2001) correctly identified 61% of predators at Northern Bobwhite (*Colinus virginianus*) nests using physical evidence at the nest site as compared to data from miniature video cameras; however, diversity of predators on his study area was small. Only 12% of predation events from Staller (2001) involved multiple predators compared to Leimgruber et al. (1994) who observed multiple predator visits (2–5 species) in 43% of predation events, a rate similar to ours. Hernandez et al. (1997) attempted to construct a dichotomous key for identification of ground-nest predators in west Texas but were not successful because of insufficient physical evidence and overlap of nest predation habits among species. Incubat-

ing Blue-winged Teal (*Anas discors*) and Mallard (*A. platyrhynchos*) hens are known to remove damaged eggs and shell fragments from the nest area following partial predation events by striped skunks (Lariviere and Walton 1998).

The relationship between ground nesting birds and nest predators is complicated, and we caution researchers to understand the limitations of using physical evidence to predict nest predator species. Our results provide insight into nest predator communities and confirm that multiple predator events are frequent (39% of the predation events recorded with cameras in our study) in the wild. Multiple predation events can greatly alter physical evidence left at the depredated nest site; thus, it is crucial that researchers test and apply any method which is used to assess nest predator communities before mitigation strategies are developed.

ACKNOWLEDGMENTS

Funding was provided by the Texas Turkey Stamp Fund through the Texas Parks and Wildlife Department, the National Wild Turkey Federation Texas State Superfund, and the Department of Wildlife and Fisheries Sciences, Texas A&M University. We thank D. B. Frels Jr. and Kerr Wildlife Management Area personnel, and Max Traweek and Region II Texas Parks and Wildlife personnel for assistance with trapping and field work. We thank all cooperating landowners and land managers for help and willingness to participate with our research. This research was conducted under Texas A&M University Animal Use Permit 2005-005.

LITERATURE CITED

Bailey, R. W. and K. T. Rinnell. 1967. Events in the turkey year. Pages 73–91 *in* The Wild Turkey and its management (O. H. Hewitt, Editor). The Wildlife Society, Washington, D.C., USA.

Baker, B. W. 1978. Ecological factors affecting Wild Turkey nest predation on south Texas rangelands. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 32:126–136.

Collier, B. A., D. A. Jones, J. N. Schaap, C. J. Randel III, B. J. Willsey, R. Aguirre, T. W. Schwertner, N. J. Silvy, and M. J. Peterson. 2007a. Survival of Rio Grande Wild Turkeys on the Edwards Plateau of Texas. Journal of Wildlife Management 71:82–86.

Collier, B. A., K. B. Melton, J. Z. Dreibelbis, W. P. Kuvlesky, G. A. Proudfoot, R. Aguirre, D. G. Hewitt, T. W. Schwertner, S. J. DeMaso, N. J. Silvy, and M. J. Peterson. 2007b. Sex ratio variation in Texas Rio Grande Wild Turkeys. Journal of Wildlife Management 71:1793–1799.

Cook, R. L. 1972. A study of nesting turkeys in the Edward's Plateau of Texas. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 26:236–244.

Davis, J. R. 1959. A preliminary progress report on nest predation as a limiting factor in Wild Turkey populations. Proceedings of the National Wild Turkey Symposium 1:138–145.

Davis, W. B. and D. J. Schmidly. 1994. The mammals of Texas. University of Texas Press, Austin, USA.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Everett, D. D., D. W. Speake, and W. K. Maddox. 1980. Natality and mortality of a north Alabama Wild Turkey population. Proceedings of the National Wild Turkey Symposium 4:117–126.

Farnsworth, G. L. and T. R. Simons. 2000. Observations of Wood Thrush nest predation in a large contiguous forest. Wilson Bulletin 112:82–87.

Gould, F. W. 1975. Texas plants: a checklist and ecological summary. Texas Agricultural Experiment Station Bulletin MP-585/Revised. College Station, USA.

Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time-specific variation in passerine nest survival: new insights into old questions. Auk 122:1–12.

Hernandez, F., D. Rollins, and R. Cantu. 1997. Evaluating evidence to identify ground-nest predators in west Texas. Wildlife Society Bulletin 25: 826–831.

Lariviere, S. 1999. Reasons why predators cannot be inferred from nest remains. Condor 101:718–721.

Lariviere, S. and L. R. Walton. 1998. Eggshell removal by duck hens following partial nest depredation by striped skunk. Prairie Naturalist 30: 183–185.

Leimgruber, P., W. J. McShea, and J. H. Rappole. 1994. Predation on artificial nests in large forest blocks. Journal of Wildlife Management 58:254–260.

Major, R. E. 1991. Identification of nest predators by photography, dummy eggs, and adhesive tape. Auk 108:190–195.

Melton, K. B. 2007. Reproductive ecology of Rio Grande Wild Turkeys on the Edwards Plateau. Thesis. Texas A&M University, College Station, USA.

Montevecchi, W. A. 1976. Egg size and the egg predatory behavior of crows. Behaviour 57:307–320.

Rader, M. J., T. W. Teinert, L. A. Brennan, F. Hernandez, N. J. Silvy, and X. B. Wu. 2007. Identifying predators and nest fates of bobwhites in southern Texas. Journal of Wildlife Management 71:1626–1630.

Randel, C. J., R. Aguirre, D. A. Jones, J. N. Schaap, B. J. Willsey, M. J. Peterson, and N. J. Silvy. 2005. Nesting ecology of Rio Grande Wild Turkey in the Edwards Plateau of Texas. Proceedings of

the National Wild Turkey Federation Symposium 9:212–218.

RANSOM JR., D., O. J. RONGSTAD, AND D. H. RUSCH. 1987. Nesting ecology of Rio Grande turkeys. Journal of Wildlife Management 51:435–439.

RICKLEFS, R. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

ROLLINS, D. AND J. P. CARROLL. 2001. Impacts of predation on Northern Bobwhite and Scaled Quail. Wildlife Society Bulletin 29:39–51.

STALLER, E. L. 2001. Identifying predators and fates of Northern Bobwhite nests using miniature video cameras. Thesis, University of Georgia, Athens, USA.

SHAFFER, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

STEPHENS, S. E., J. J. ROTELLA, M. S. LINDBERG, M. L. TAPER, AND J. K. RINGELMAN. 2005. Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. Ecological Applications 15:2137–2149.

TREVOR, J. T., R. W. SEABLOOM, AND R. D. SAYLER. 1991. Identification of mammalian predators at artificial waterfowl nests. Prairie Naturalist 23:93–99.

WESTERSKOV, K. 1950. Methods for determining the age of game bird eggs. Journal of Wildlife Management 14:56–67.

WHITE, G. C. AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

The Wilson Journal of Ornithology 120(4):910–913, 2008

No Evidence for Spring Re-introduction of an Arbovirus by Cliff Swallows

Valerie A. O'Brien,[1] Amy T. Moore,[1] Kathryn P. Huyvaert,[2] and Charles R. Brown[1,3]

ABSTRACT.—We sampled 100 Cliff Swallows (*Petrochelidon pyrrhonota*), just after arrival in Nebraska breeding areas, to ascertain if migrating birds re-introduce Buggy Creek virus (BCRV; Togaviridae) to north-temperate localities in spring. Most birds sampled were previously banded and were known to have used parasite-free nesting colonies in past summers and/or were seronegative to BCRV; thus, they were unlikely to have been previously exposed to the virus in their breeding areas. None of the birds had evidence of viral RNA in blood, as measured by RT-PCR. These results are consistent with other studies that have shown little evidence that migratory birds re-introduce arboviruses to temperate localities between years. *Received 14 February 2008. Accepted 5 May 2008.*

Whether arthropod-borne viruses (arboviruses) are re-introduced in spring by migratory birds in temperate latitudes is a major question in the study of bird-associated viruses (Reeves 1974, Scott and Weaver 1989, Crans et al. 1994). Arboviruses are rarely found in over-wintering insect vectors such as mosquitoes (Rosen 1987, Reeves 1990, Day 2001), and the conventional wisdom is that infected birds from the tropics—that are fed upon by insect vectors (e.g., mosquitoes) after arrival in breeding areas—may provide a mechanism for annual recurrence of virus in temperate latitudes of central and northern North America (Cilnis et al. 1996, Unnasch et al. 2006). Empirical evidence for this scenario is limited, however, and consists mostly of a few records of birds (bound for unknown destinations) with eastern equine encephalomyelitis virus when captured in spring after crossing the Gulf of Mexico (Calisher et al. 1971). Demonstrating virus re-introduction requires sampling birds upon their arrival at breeding sites sufficiently early in the nesting season that re-infection by local vectors can be excluded if positive birds are found. No studies have systematically surveyed newly arrived migratory birds for arboviruses.

Buggy Creek virus (Togaviridae, *Alphavirus*) is an unusual arbovirus vectored primarily by the swallow bug (Hemiptera: Cimicidae: *Oeciacus vicarius*), an ectoparasite of the

[1] Department of Biological Sciences, University of Tulsa, Tulsa, OK 74104 USA.

[2] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523 USA.

[3] Corresponding author; e-mail: charles-brown@utulsa.edu

colonially nesting Cliff Swallow (*Petrochelidon pyrrhonota*). Vertebrate hosts for Buggy Creek virus (BCRV) are Cliff Swallows and House Sparrows (*Passer domesticus*) that occupy nests in swallow colonies (Hayes et al. 1977, Scott et al. 1984). A related alphavirus, Fort Morgan virus, is a strain of BCRV (Pfeffer et al. 2006). BCRV, although not documented to affect humans, is phylogenetically and serologically related to western equine encephalomyelitis virus (WEEV) (Calisher et al. 1988, Powers et al. 2001), and WEEV affects both people and livestock (Reisen and Monath 1989). Birds have been suggested to move WEEV between North and South America (Weaver et al. 1997).

We sampled Cliff Swallows for virus immediately after the birds' arrival at breeding sites in southwestern Nebraska, USA as part of our efforts to understand the population dynamics of BCRV and its association with Cliff Swallows (Brown et al. 2001; Moore et al. 2007; Brown et al. 2007, 2008). Our objective was to examine whether these birds were infected with BCRV upon their return and could potentially re-introduce the virus to their breeding areas.

Cliff Swallows breed throughout much of North America, nesting in large colonies underneath cliff overhangs and bridges, and winter in southern Brazil, Uruguay, and northern Argentina (Brown and Brown 1995). BCRV occurs annually in our Nebraska study area and is commonly isolated from the insect vectors (Brown et al. 2001, 2007; Moore et al. 2007). Its predictable annual occurrence suggests the virus either over-winters in swallow bugs and/or in resident House Sparrows, or is re-introduced each season by Cliff Swallows when they return from their winter range in South America.

METHODS

Long-term work in our study area (in Keith, Garden, Lincoln, and Morrill counties, Nebraska) indicates the first Cliff Swallows appear on about 18 April each year with numbers slowly increasing during the following 10 days (Brown and Brown 1996: 443). The first arrivals tend to concentrate at the same 2–3 colony sites in the study area (C. R. Brown, pers. obs.). We mist-netted Cliff Swallows between 23 and 29 April 2006 and 2007 at two colony sites (41° 15′ N, 101° 37′ W; 41° 13′ N, 101° 37′ W) that contained most birds present in the study area at that time. The early sampling dates ensured that birds at both sites were newly arrived. Both colony sites sampled had been fumigated multiple times per summer during the previous 10 seasons to remove swallow bugs, suggesting that few bugs were present in April and the likelihood of any bird being infected by a bug after arrival and before sampling was low. The insecticide used is highly effective against swallow bugs (Brown and Brown 2004). Fumigation procedures are described by Brown and Brown (1996).

Birds caught were bled by jugular or brachial venipuncture, in which 0.1 ml of blood was collected and placed in 0.4 ml of BA-1 diluent (Moore et al. 2007). Samples were centrifuged and 25 μl of supernatant was added to 100 μl of a guanidine thiocyanate-based lysis buffer. RNA was extracted after the addition of 100 μl of 100% ethanol using the QIAmp Viral RNA Mini Kit (Qiagen), following the manufacturer's protocol. A positive BCRV control was included in each extraction.

Reverse-transcription PCR (RT-PCR) was performed using the OneStep RT-PCR Kit (Qiagen) following the manufacturer's protocol. We used BCRV-specific primers that yielded a 208-bp fragment from the E2 region of the viral genome. Primer sequences and thermocycler conditions are described in Moore et al. (2007). Product (6.5 μl) was electrophoresed on a 4% Nusieve/agarose gel to identify any positive pools, using at least one BCRV positive control on each gel and a 100-bp ladder. This protocol was used for detecting BCRV in both swallow bug pools and sera of nestling House Sparrows, which are commonly infected (about 25% of bug pools and >20% of nestling sparrows; Moore et al. 2007; V. A. O'Brien and C. R. Brown, unpubl. data). Our RT-PCR methods have also detected BCRV in sera of Cliff Swallows during the summer nesting season, including samples confirmed by both RT-PCR and plaque assay on Vero cells (V. A. O'Brien and C. R. Brown, unpubl.data).

RESULTS

We captured 100 Cliff Swallows during the sampling periods in the 2 years. None of the 100 birds had evidence of circulating BCRV

RNA in blood, as judged from RT-PCR. All but 14 birds had been banded in the study area in a previous breeding season. Eighty-one were at least 2 years of age and their history of breeding-colony use was known for at least one previous year. Five had been banded the previous year as recently fledged juveniles. Fifty-nine of the 86 birds with past histories were known to have been resident at only fumigated colonies in the past (the same sites sampled in this study), 13 had used only non-fumigated sites in the past, and 9 had used both fumigated and non-fumigated sites in previous seasons. The 5 juveniles had been captured at fumigated colonies a few days after fledging.

DISCUSSION

Birds that had used parasite-free sites in past seasons were unlikely to have been exposed to BCRV in a previous summer and therefore not likely to show latent, chronic infections (as seen for some arboviruses; Reisen et al. 2003). The 47 birds sampled in 2007 were tested for BCRV-specific antibodies using a plaque reduction neutralization test (Huyavert et al. 2008); none of these birds was seropositive (G. R. Young and N. Komar, pers. comm.). Thus, the individuals sampled in this study were well suited to studying whether virus could be introduced by migrants that were infected prior to arrival in breeding areas.

Hayes et al. (1977) sampled 52 adult Cliff Swallows for the Fort Morgan strain of BCRV on 30 May 1974 in northeastern Colorado, ~215 km from our study area. That study used plaque assay and found no evidence of BCRV in swallows. Hayes et al. (1977) concluded that no evidence existed for spring re-introduction of virus by returning birds, although their samples were taken sufficiently late in the season that birds had begun egg-laying at time of sampling. Using a more sensitive assay (RT-PCR), we also found no evidence of circulating BCRV (i.e., viral RNA) in blood of adult Cliff Swallows, and our birds had arrived at most only a few days before sampling.

Most birds we sampled had probably not been exposed to BCRV in breeding areas, by virtue of their use of fumigated colony sites in past years (and, for some, their lack of antibodies to BCRV). Thus, they were prime candidates for transporting virus from wintering areas or from stopover sites en route. Surveys for BCRV have not been conducted in South America, and whether it occurs in wintering areas is unknown. BCRV is found at Cliff Swallow colony sites south of our study area, for example in west central Oklahoma, about 750 km from the Nebraska study area (Hopla et al. 1993; C. R. Brown, V. A. O'Brien, and A. T. Moore, unpubl. data). Migrating Cliff Swallows conceivably could be infected there and move the virus north to Nebraska.

Our results are consistent with the absence of direct evidence that migrating birds, re-introduce arboviruses to temperate localities. It is more likely these viruses persist annually by over-wintering in insect vectors or alternative resident hosts. Over-wintering of BCRV in swallow bugs is known to occur (Hayes et al. 1977, Rush et al. 1980, Strickler 2006). House Sparrows may be more suitable hosts for BCRV than Cliff Swallows, at least in summer (V. A. O'Brien and C. R. Brown, unpubl. data), and may provide another mechanism for annual persistence of virus. This is especially true if BCRV is maintained via latent, chronic infections in vertebrate tissue over long periods of time (Huyvaert et al. 2008). The role of migratory birds in re-introducing arboviruses to temperate latitudes in spring is unclear, and we urge all studies finding even negative evidence for re-introduction be reported.

ACKNOWLEDGMENTS

We thank the School of Biological Sciences of the University of Nebraska for use of the Cedar Point Biological Station; Ginger Young, Nicholas Komar, and the Centers for Disease Control for serological results; and C. E. Braun, R. E. Carleton, and an anonymous reviewer for helpful suggestions on the manuscript. This work was supported by the National Science Foundation (0514824) and the National Institutes of Health (AI057569).

LITERATURE CITED

Brown, C. R. and M. B. Brown. 1995. Cliff Swallow (*Hirundo pyrrhonota*). The birds of North America. Number 149.

Brown, C. R. and M. B. Brown. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, Illinois, USA.

Brown, C. R. and M. B. Brown. 2004. Empirical measurement of parasite transmission between groups in a colonial bird. Ecology 85:1619–1626.

Brown, C. R., M. B. Brown, A. T. Moore, and N.

Komar. 2007. Bird movement predicts Buggy Creek virus infection in insect vectors. Vector-Borne and Zoonotic Diseases 7:304–314.

Brown, C. R., N. Komar, S. B. Quick, R. A. Sethi, N. A. Panella, M. B. Brown, and M. Pfeffer. 2001. Arbovirus infection increases with group size. Proceedings of the Royal Society of London, Series B 268:1833–1840.

Brown, C. R., M. B. Brown, A. Padhi, J. E. Foster, A. T. Moore, M. Pfeffer, and N. Komar. 2008. Host and vector movement affects genetic diversity and spatial structure of Buggy Creek virus (Togaviridae). Molecular Ecology 17:2164–2173.

Calisher, C. H., K. S. C. Maness, R. D. Lord, and P. H. Coleman. 1971. Identification of two South American strains of eastern equine encephalomyelitis virus from migrant birds captured on the Mississippi delta. American Journal of Epidemiology 94:172–178.

Calisher, C. H., N. Karabatsos, J. S. Lazuick, T. P. Monath, and K. L. Wolff. 1988. Reevaluation of the western equine encephalitis antigenic complex of alphaviruses (family Togaviridae) as determined by neutralization tests. American Journal of Tropical Medicine and Hygiene 38:447–452.

Cilnis, M. J., W. Kang, and S. C. Weaver. 1996. Genetic conservation of Highlands J viruses. Virology 218:343–351.

Crans, W. J., D. F. Caccamise, and J. R. McNelly. 1994. Eastern equine encephalomyelitis virus in relation to the avian community of a coastal cedar swamp. Journal of Medical Entomology 31:711–728.

Day, J. F. 2001. Predicting St. Louis encephalitis virus epidemics: lessons from recent, and not so recent, outbreaks. Annual Review of Entomology 46: 111–138.

Hayes, R. O., D. B. Francy, J. S. Lazuick, G. C. Smith, and E. P. J. Gibbs. 1977. Role of the Cliff Swallow bug (*Oeciacus vicarius*) in the natural cycle of a western equine encephalitis-related alphavirus. Journal of Medical Entomology 14:257–262.

Hopla, C. E., D. B. Francy, C. H. Calisher, and J. S. Lazuick. 1993. Relationship of Cliff Swallows, ectoparasites, and an alphavirus in west-central Oklahoma. Journal of Medical Entomology 30: 267–272.

Huyvaert, K. P., A. T. Moore, N. A. Panella, E. A. Edwards, M. B. Brown, N. Komar, and C. R. Brown. 2008. Experimental inoculation of House Sparrows (*Passer domesticus*) with Buggy Creek virus. Journal of Wildlife Diseases 44:331–340.

Moore, A. T., E. A. Edwards, M. B. Brown, N. Komar, and C. R. Brown. 2007. Ecological correlates of Buggy Creek virus infection in cimicid swallow bugs *Oeciacus vicarius*, southwestern Nebraska, 2004. Journal of Medical Entomology 44:42–49.

Pfeffer, M., J. E. Foster, E. A. Edwards, M. B. Brown, N. Komar, and C. R. Brown. 2006. Phylogenetic analysis of Buggy Creek virus: evidence for multiple clades in the western Great Plains, United States of America. Applied and Environmental Microbiology 72:6886–6893.

Powers, A. M., A. C. Brault, Y. Shirako, E. G. Strauss, W. Kang, J. H. Strauss, and S. C. Weaver. 2001. Evolutionary relationships and systematics of the alphaviruses. Journal of Virology 75:10118–10131.

Reeves, W. C. 1974. Overwintering of arboviruses. Progress in Medical Virology 17:193–220.

Reeves, W. C. 1990. Epidemiology and control of mosquito-borne arboviruses in California, 1943–1987. California Mosquito Vector Control Association, Sacramento, USA.

Reisen, W. K. and T. P. Monath. 1989. Western equine encephalomyelitis. Pages 89–137 *in* The arboviruses: epidemiology and ecology. Volume 5 (T. P. Monath, Editor). CRC Press, Boca Raton, Florida, USA.

Reisen, W. K., R. E. Chiles, V. M. Martinez, Y. Fang, and E. N. Green. 2003. Experimental infection of California birds with western equine encephalomyelitis and St. Louis encephalitis viruses. Journal of Medical Entomology 40:968–982.

Rosen, L. 1987. Overwintering mechanisms of mosquito-borne arboviruses in temperate climates. American Journal of Tropical Medicine and Hygiene 37(Supplement):69S–76S.

Rush, W. A., D. B. Francy, G. C. Smith, and C. B. Cropp. 1980. Transmission of an arbovirus by a member of the Family Cimicidae. Annals of the Entomological Society of America 73:315–318.

Scott, T. W. and S. C. Weaver. 1989. Eastern equine encephalomyelitis virus: epidemiology and evolution of mosquito transmission. Advances in Virus Research 37:277–328.

Scott, T. W., G. S. Bowen, and T. P. Monath. 1984. A field study on the effects of Fort Morgan virus, an arbovirus transmitted by swallow bugs, on the reproductive success of Cliff Swallows and symbiotic House Sparrows in Morgan County, Colorado, 1976. American Journal of Tropical Medicine and Hygiene 33:981–91.

Strickler, S. A. 2006. Winter ecology of a bird-associated arbovirus. Thesis. University of Tulsa, Tulsa, Oklahoma, USA.

Unnasch, R. S., E. W. Cupp, and T. R. Unnasch. 2006. Host selection and its role in transmission of arboviral encephalitides. Pages 73–89 *in* Disease ecology: community structure and pathogen dynamics (S. K. Collinge and C. Ray, Editors). Oxford University Press, Oxford, United Kingdom.

Weaver, S. C., W. Kang, Y. Shirako, T. Rümenapf, E. G. Strauss, and J. H. Strauss. 1997. Recombinational history and molecular evolution of western equine encephalomyelitis complex alphaviruses. Journal of Virology 71:613–623.

The Wilson Journal of Ornithology 120(4):914–915, 2008

Marbled Godwit Collides with Aircraft at 3,700 m

Carla J. Dove[1,3] and Court Goodroe[2]

ABSTRACT.—On 25 August, 2007, a Marbled Godwit (*Limosa fedoa*) was struck by a Southwest Airlines Boeing 737 at 3,700 m. The bird was identified by examination of feather remains recovered from the aircraft and represents an altitude record for this species. *Received 13 December 2007. Accepted 12 April 2008.*

Bird/aircraft collisions (birdstrikes) are an increasing hazard to aviation safety and cause millions of dollars of damage to both civil and military aviation each year (Dolbeer et al. 2000). Height distributions of major groups of birds that collide with aircraft have been recently investigated using data from civil aircraft birdstrikes, but attempts to make species comparisons with these data were not possible because only ~23% of the birdstrikes above 152 m were identified to the species level (Dolbeer 2006). Increasing the percentage of birds identified to species that are involved in birdstrikes will improve techniques used to reduce birdstrikes as well as aid in our understanding of flight patterns and altitudes of different species of birds.

We describe the identification of a high altitude birdstrike involving a Marbled Godwit (*Limosa fedoa*) with an aircraft that had taken off from El Paso, Texas, USA.

OBSERVATIONS

On 25 August 2007, a Southwest Airlines Boeing 737 aircraft struck a bird at 1051 hrs MDT. The bird was struck just east of El Paso, Texas during the 'climb' phase of flight on departure. The altitude was recorded by the flight crew at the time of the strike at about 3,700 m above ground level. The plane returned to El Paso, landing 24 min after takeoff with damage to the left horizontal stabilizer, fuselage, and radome. Sufficient feather remains from the wings and body of the bird were salvaged and submitted to the Smithsonian Institution. The bird was identified as a Marbled Godwit based on color patterns and size of the feathers in comparison with museum specimens. It is unknown how many birds were struck or if additional species were involved in this event.

DISCUSSION

This is the highest known altitude record for a godwit. The next highest record was a Bar-tailed Godwit (*Limosa lapponica*) found dead on Mt. Ruapehu (New Zealand) by hikers at 2,610 m in January 2006 (Battley and Horn 2006). Previous published high altitude birdstrike records identified to the species level include Ruppell's Vulture (*Gyps rueppellii*) at 11,300 m (Laybourne 1974), and Mallard (*Anas platyrhynchos*) at 6,400 m (Manville 1963). The Marbled Godwit involved in this birdstrike was within the range of the southern fall migration for this species (Gratto-Trever 2000) and documents that a fairly short-distance migrant can attain high flight altitudes during migration. Accurate birdstrike reporting detailing such data as in this event, together with molecular techniques that now aid in species level identifications from blood and tissue samples, will improve ornithological knowledge of flight altitudes of birds.

ACKNOWLEDGMENTS

We thank the Southwest Airlines crew for accurately reporting this birdstrike. M. A. Heacker and N. C. Rotzel assisted with the bird identification.

LITERATURE CITED

BATTLEY, P. F. AND C. HORN. 2006. A high-altitude Bar-tailed Godwit (*Limosa lapponica*) on Mt Ruapehu, North Island, New Zealand. Notornis 53:381–382.

DOLBEER, R. A. 2006. Height distribution of birds recorded by collisions with civil aircraft. Journal of Wildlife Management 70:1345–1350.

DOLBEER, R. A., S. E. WRIGHT, AND E. C. CLEARY,

[1] National Museum of Natural History, MRC 116, P. O. Box 37012, Washington, D.C. 20013, USA.

[2] Southwest Airlines Company, 2702 Lovefield Drive, Dallas, TX 75235, USA.

[3] Corresponding author: e-mail: dovec@si.edu

2000. Ranking the hazard level of wildlife species to aviation. Wildlife Society Bulletin, 28:372–378.

Gratto-Trever, C. L. 2000. Marbled Godwit (*Limosa fedoa*). The birds of North America. Number 492.

Laybourne, R. C. 1974. Collision between a vulture and an aircraft at an altitude of 37,000 feet. Wilson Bulletin 86:461–462.

Manville, R. H. 1963. Altitude record for Mallard. Wilson Bulletin 75:462.

The 2008 William and Nancy Klamm Service Award

In 1953, a young man from Steubenville, Ohio, attended his first Wilson Ornithological Club meeting with his parents. This was the beginning of a more than fifty-year relationship between Richard C. Banks and the Wilson Ornithological Society. Dick joined the Wilson Ornithological Society in 1959 as a graduate student, and since then his service has been varied and extensive. He has been active on numerous committees including the Wilson Prize Committee, selection committee for the Fuertes, Nice, and Stewart Awards, Publications Committee, Scientific Program Committee, and the Resolutions Committee, and in many instances he served as Chair of the committee. He has served as an elected Council member (1979–1982), Second Vice-President (1987–1989), First Vice-President (1989–1991), and President of the Society (1991–1993). During his presidency, Dick established the Committee on Undergraduate Outreach to help stimulate an interest in ornithology among undergraduate students, and to help maintain and focus that interest to stimulate students to continue studies in ornithology. He was the first editor of the *Ornithological Newsletter*, which was established as a quarterly publication in 1976 and led to the formation of the Ornithological Societies of North America (OSNA). He continued as editor of the newsletter until 1989. He co-chaired the Local Committee for the 2005 annual meeting in Beltsville, Maryland. He has given his time reviewing many manuscripts for the *Wilson Bulletin*, and has also made more tangible donations, both to the Van Tyne library and the Centennial Fund. Dick continues to be very active on Wilson Council, and has modeled professional behavior and responsibility for many Wilson members at various stages in their careers. He is a staunch supporter of ornithology, ornithologists, and the Wilson Ornithological Society. It is with the utmost respect and gratitude that we present the 2008 William and Nancy Klamm Service Award to Richard C. Banks.—Sara R. Morris, W. E. Davis Jr., Jerome A. Jackson, John Kricher, and Doris Watt (Klamm Service Award Committee).

The Wilson Journal of Ornithology 120(4):917–926, 2008

Ornithological Literature

Compiled by Mary Gustafson and Robert B. Payne

THE MEINERTZHAGEN MYSTERY: THE LIFE AND LEGEND OF A COLOSSAL FRAUD. By Brian Garfield. Potomac Books Inc., Washington, D.C., USA. 2007: xiv + 353 pp, 14 black and white photographs. ISBN 978-1-59797-041-9. $19.25 (hardcover). ISBN 978-1-59797-160-7. $12.57 (paper).—Richard Meinertzhagen (1878–1967) spurned a career in the family banking business to join the British military, attaining the rank of colonel, and in 1921 was transferred to the Foreign Office, where he fancied himself to have been engaged mainly in espionage. Most of his postings in both capacities were overseas in Africa and Asia, and he boasted and wrote expansively on his exploits as a warrior and spy. Along the way he nurtured a passion for natural history, amassed a large personal collection of birds, and published books and papers in ornithological journals. He also stole specimens of birds from museum collections, fabricated label data for them, and published deliberately falsified information about birds in scientific journals—facts that have only been brought to light in recent years through painstaking research and scientific investigation. Many of us in the museum community who had long been aware of Meinertzhagen's ornithological perfidies had come to wonder if the rest of his history might prove to be just as grand a prevarication.

Brian Garfield set out to answer exactly that question because, in his words: "The precision and energy that scientists invested in reexamining his zoological cons were not replicated in other circles. There was no effort to verify and collate his separate parallel paths." In short, as the subtitle makes clear, Meinertzhagen's entire legacy proves to be a gigantic lie. Although he was "a noted figure in science, war, and espionage . . . in all three fields he also was a fantasist who perpetrated colossal deceptions."

Garfield, according to his rather robustious web site, is mainly a prolific American writer of crime and mystery fiction whose considerable success hinges on his insistence on entertaining the reader. That is not necessarily the best qualification for a historian, even though Meinertzhagen's egregious outrages make his history more entertaining than most. One will find attributions for which no source is cited and conclusions based on evidence that at times seem less than satisfactory. But this is partly due to the nature of lies themselves, as it is much more difficult to prove that someone didn't commit a particular act than to prove that he did. Thus, much of Garfield's case against Meinertzhagen rests on the fact that no corroboration can be found for practically any of his alleged major deeds as a warrior and spy.

As might be expected, Garfield has little understanding of ornithologists or what they do in museums. He confuses taxonomy and taxidermy. Hugh Whistler (whose bird skins numbered some 17,000) and other scientific ornithologists are referred to as "birders." Meinertzhagen's activity in museums in London, Tring, and Berlin is said to have been "cataloging birds." It should be Erwin, not Irwin Stresemann, etc.

Meinertzhagen was a compulsive chronicler of himself. But his in-law Malcolm Muggeridge considered that Meinertzhagen's "copious diaries . . . in elegant leather [that] adorned the walls of his study . . . would prove to be a monument to his fantasy self." And so it appears. There seem to have been no original journals kept in the field, at least none that survived, and only the fictitious fantasies remain.

One very interesting document that Garfield cites is a 66-page typescript entitled "Conquisitio Mea. A Record of my Ornithological Activities and Collections." In 1942, Meinertzhagen sent this to Alexander Wetmore, then Assistant Secretary of the Smithsonian Institution, with a view towards having it published in the United States. "Conquisitio" is Latin for "a bringing together" but can also mean "collecting." The first 11 pages consist of a brief history of Meinertzhagen's collecting, his methods of preparing and storing

specimens, his philosophy of nomenclature, etc. The rest treats specimens that he considered to be the highlights of his collection, some of them now known to have been stolen. Before returning the manuscript in 1944, Wetmore had a copy made to insure its preservation in the event of the sinking of a mail ship or similar calamity. In all likelihood, however, he would also have harbored suspicions about Meinertzhagen's veracity and probably wanted to insure that a copy was preserved for posterity. I examined this document in the Smithsonian Archives and found that it is not a "photocopy" as Garfield states, but a laborious retyping of the entire manuscript by an extremely talented stenographer. Its importance lies in the fact that this "is one of the few documents of length from the period that [Meinertzhagen] did not have an opportunity to destroy or revise beyond recognition" (page 260, note 19).

Garfield cites the Conquisitio (hereafter CqM) in the following passage (page 47):

> In the 1940s he wrote, intending this for publication, that in June 1897 he went trekking into Lapland on a camping-birding expedition. In the same document he wrote that his brother Dan had gone into Lapland a year later, in 1898. Perhaps we are meant to infer that brother Dan was copying Richard's trail-blazing pioneer work. In fact, it was Dan who went north through Scandinavia into Lapland in 1897. Richard did not go there until many years later; in 1897 he was at work in the bank in London.

On the same page Garfield also refers to Meinertzhagen's "clumsy later attempt to purloin credit for the Lapland expedition" as suggesting that the relationship with his brother "may have been shaded with envy." Unfortunately for the truth of Garfield's claim, there is absolutely no mention whatever in CqM of Richard going to Lapland in 1897. His first foreign collecting after escaping the "miserable slavery" of the bank appears to have been as a "junior subaltern of a British Regiment in the deserts of Rajputana" (CqM, page 4). Leading the list of "Collecting Areas" represented in his collection is: "1898 My brother Dan made a trip to Arctic Lapland, returning with a large collection of eggs and several skins" (CqM, page 6). 1898 is erroneous for the date of collection, but being the year of Dan's death it could easily be viewed as the date obtained by Richard. Therefore, if Meinertzhagen actually asserted that he had been to Lapland in 1897, we are left to guess where he may have done so. Dan's death was a traumatic event in Meinertzhagen's life so that "purloining" credit for the Lapland expedition is a potent accusation that for now remains undocumented. Was this the result of faulty memory, bad organization of notes, or some other deficiency in Garfield's scholarship?

Garfield tells us that Meinertzhagen wrote "that both Thomas Huxley and Charles Darwin were quite fond of him, and that Darwin dandled Richard on his knee" (page 41). He rightly questions the dandling as being highly unlikely. But he fails to document where Meinertzhagen made such a statement, which a careful historian would surely have footnoted. The assertion happens to come from CqM and Garfield could have had a lot more fun with it than he did, as the passage epitomizes Meinertzhagen's infinite capacity for lying. "The passion for birds was born in my brother Dan and myself. At an early age we pored over Gould's Birds of Great Britain and, later on, over Lilford's Birds of the British Islands, until we knew every bird by name and sight. It was about then that we sat in the laps of two venerable white-haired old gentlemen, Professors Huxley and Darwin, and at the feet of Henry Seebohm, fresh from his discovery of the breeding grounds of the Grey Plover" (CqM, pages 1–2). Let's apply a little chronology to this farrago of nonsense: RM was born in 1878, the reclusive Darwin died four years later in 1882 after years of debilitating illness, the first volume of Lilford's work appeared in 1885 to be finished posthumously in 1897, and Seebohm discovered the Grey Plover's nest in 1875, three years before Meinertzhagen was born.

In addition to being a thief and habitual liar, there is a cloud of plagiarism, attributed to an anonymous source, over Meinertzhagen's book on birds of Egypt and, as had been documented before, over parts of his book on Arabian birds as well. Far worse, however, is the suspicion, well-justified in my opinion,

that Meinertzhagen was a wife-killer. His second wife, Annie Jackson, was an accomplished ornithologist in her own right before marrying Richard, and was active in museum and field, being a crack shot. But she evidently caught on to Richard's lying ways and was aware that he was publishing false information about Asian birds and stood to expose him. She changed her will to exclude Richard in favor of their children and shortly thereafter, on her remote estate in Scotland, was killed by a single pistol bullet that penetrated her head and spine. Richard was the only other person present.

Garfield obtained the police reports (which had wrongly been rumored to have been ordered to be kept sealed for some long period of time) and reviewed the evidence and opinions of this shocking episode, ultimately concluding that (pages 171–172): "For the record, RM is innocent until and unless he should be proven guilty. . . . The case for RM's innocence derives in part, and with irony, from his habit of lying." That is, because all of his tales about killing people in wars were shown by Garfield to be unsubstantiated. Thus, the argument begins to take on the aspect of a school logic problem—given that a person always tells a lie, determine which of the following of his statements must therefore be true. There was never any suggestion that Annie was suicidal. The local papers, presumably reflecting what Meinertzhagen told the police, reported the case as an accident and Meinertzhagen wrote in his diaries that he and Annie had been at target practice, he had gone to retrieve a target and heard a shot behind him, turned and saw Annie dead on the ground. Later he evidently told more than one person that they had had a duel. If the assumption is that Meinertzhagen always lied, then his wife did not die in an accident or a duel. Ergo, he killed her. So much for the lying defense.

Meinertzhagen was long infatuated with his much younger cousin Theresa Clay, who, following Annie's death in 1928, became Richard's collaborator and companion. Theresa went on to become an authority on bird ectoparasites, although she was evidently complicit in fabricating data with Meinertzhagen, which bears more comprehensive investigation.

Meinertzhagen had first been caught stealing bird specimens from the British Museum in 1919 and was banned from the collection until Walter Rothschild interceded on his behalf and he was readmitted in 1921, whereafter he continued to steal from that and other collections, although he was long held in suspicion by British Museum administrators. He was also caught stealing books and valuable color plates and Garfield relates that the police were called in on more than one occasion but charges were never filed. Some of Meinertzhagen's bogus war exploits were incorporated into military histories and are still perpetuated. On and on he went, unchecked, protected by his status in society, his intimidating personality, and the phlegmatic British aversion to creating any sort of unpleasant disturbance.

Garfield (page 10) alludes to a class "cover-up" and this cover-up appears still be in effect. It is a disturbing aspect of his book that so much is attributed to anonymous sources. Many of those now willing to cast Meinertzhagen in a negative light still do not wish to be identified. A long quote about how Meinertzhagen perpetrated his Asian frauds and Annie realizing what he had done is from a "key ornithological source, who has asked for anonymity" (page 169). A "lady ornithologist" reports that Meinertzhagen asked her on a mountain climbing date in a "deadly voice" and opined that he was a mad man and had murdered his wife (page 171). On the same page, the rumor of a duel is reported in "a recorded interview [with] one of Meinertzhagen's relatives." An endnote in this passage does not identify the relative nor say where the recording may be housed but merely reports more suspicions from "a well known science journalist" and "another of his relations" (page 303, note 37). Two notes down, a motive for Annie's killing is "offered by an ornithologist who wrote to me on 17 June 2006." Why is the date important if the name is omitted?

A long note about the late South African ornithologist P. A. Clancey's relationship with Meinertzhagen "is related third-hand by various sources" (page 327, note 12), which is certainly how Garfield must have received the report that Clancey "traveled with RM on safari in 1948–49, and later reported RM's noc-

turnal sprees to several fellow ornithologists, apparently including Storrs Olson" (page 311, note 7). Nowhere is there an indication of the identity or significance of Storrs Olson. A well-known curmudgeonly ornithologist, who shall go unnamed, reports to the readers of this review that Storrs Olson has only a distant memory of meeting Clancey and no recollection whatever of anything that he may have said.

Near the end of his text, Garfield characterizes the whole saga in a pithy summation: "From a sociological angle the Meinertzhagen story makes for a fascinating study of ruling-class dynamics. From a psychiatric angle it makes for an eye-popping case study in narcissistic pathology" (page 246). I trust his explanation that his book was "not written to settle scores or to right personal wrongs. It is an examination of a life that was lived and then revised and then believed" (page 251, note 7). Its various shortcomings aside, Garfield's book is a sterling contribution towards unraveling the Meinertzhagen mystery and it provides powerful testimony in support of the fact that we cannot believe a word that Richard Meinertzhagen ever wrote or said about anything. But we also need to be wary of what has been written about him by others as well.—STORRS L. OLSON, Curator, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA; e-mail: olsons@si.edu

LOST WORLDS: ADVENTURES IN THE TROPICAL RAINFOREST. By Bruce M. Beehler. Yale University Press, New Haven, Connecticut, USA. 2008: 258 pages, 11 black-and white wash paintings, 10 maps, and 19 black-and-white photographs. ISBN: 978-0-300-12228-2. $28.00 (cloth).—This book is the story of Bruce Beehler's more than 30 years of research and conservation work in rainforests around the world. It is a book of adventure in wild places, and the scientific and socio-political lessons learned in the turmoil of conservation efforts in developing nations. Beehler is an ornithologist and much of what he presents has an ornithological focus. The book consists of a Preface, an Introduction, 10 chapters, an Epilogue, a Bibliography, and an Index. The Preface begins in a rainforest camp setting in Papua (western New Guinea, formally Irian Jaya), Indonesia, where he is escaping a desk job working for the U.S. Department of State. He explores his reasons for being there, and the explanation sets the tenor for the rest of the book: ". . . it was the absolute necessity of determining how the best of these rainforests could be preserved for generations to come—so that our great-grandchildren could hear the rainforest whisper its secrets.". . . "This book, then, is a story of the rainforest and its overlooked importance to humankind's long-term well-being."

Chapter 1, In the Rainforest, traces Beehler's initial encounter with the rainforests of Papua New Guinea (eastern New Guinea) in 1975, brought there by the allure of birds of paradise, bowerbirds, honeyeaters, and cassowaries. He recounts his adventures in field camps, conversing with natives in Neomelanesian Pidgin, and in general learning the ways of the rainforest, its birds and people. Chapter 2, In the Zone and on the Plantation, takes the reader half a world away from New Guinea to Panama and the famous Pipeline road near which his group from Princeton University camped. He compares the similarities with New Guinea rainforests (e.g., domination by a canopy of hardwoods, lots of vines and lianes) and contrasts the differences (e.g., the presence of monkeys in Panama, and the presence of an indigenous forest-dwelling people in New Guinea). The scene then shifts to the rainforests of India in Chapter 3, On the Trail of Ripley and Ali, and Chapter 5, Biodiversity and Intrigue across the Inner Line. In 1981 Beehler had joined S. Dillon Ripley, Secretary of the Smithsonian Institution as Ripley's scientific assistant, and for a decade set up Ripley's bird surveys in India. He recounts his difficulties with the Indian bureaucracy, habitat alteration on a grand scale, and his interactions with Ripley and Sálim Ali, the dean of Indian ornithologists with whom Ripley had worked for four decades. The "Inner Line" is the politically sensitive frontier where foreigners are not usually allowed. Here Beehler encountered hostility, due in part to a negative reaction to perceived "sci-

entific imperialism" practiced by first world scientists.

In Chapter 4, Wallace's Promised Island, a pleasant interlude on the Atherton Tableland of Queensland, Australia, is followed by a disastrous visit to a Freeport mining camp high in the mountains of Papua (Irian Jaya), where they were kept under virtual house arrest by the Indonesian military and not allowed to conduct the bird surveys they were there to do. By 1999 Beehler was working with Counterpart International, a non-governmental organization, on a project called Forest Gardens, an experimental agroforestry program that encouraged tropical rural farmers to conserve standing forest through a system akin to growing shade coffee. Beehler visited Ivory Coast in West Africa (Chapter 6), and reports on the conservation difficulties posed by the continual movements of landless displaced people and the resultant clearing of forests by squatters. Ivory Coast experienced the strife and political disintegration that threaten conservation projects throughout the developing world.

In Chapter 7, Local People Really Do Count, Beehler recounts an expedition to Papua New Guinea in 1993 (he has visited New Guinea 40 times) to a field camp on the Nagore River. He describes the camp life in detail, and then analyzes the conservation lessons that he learned there, which include the mistake of underestimating the local people and their commitment to conserving their forest (they have been doing it for centuries). The message to take away is that local people are critical for successful conservation initiatives. Chapter 8, Pitiful Scraps of Forest, deals with a Forest Gardens restoration project on Cebu Island in the Philippines, a place plagued by problems of landless migrants that had squatted and destroyed much of central Cebu National Park, due in part to lack of any decisive government oversight. Beehler comments: "No question, the single greatest threat to the world's rainforests is population. . . . If the world cannot manage its population in a rational way through smart family planning and strong economic incentives, problems galore are ahead for the earth's remaining rainforests."

Chapter 9, Lemurs, Vangas, Chameleons, and Poverty, describes the conservation problems in another impoverished island, Madagascar. We learn of lemurs (endemic primates) and endemic families of birds in the rich remnant fragments of rainforest, but are reminded that these remnants are in a sea of human-devastated landscape, deforested to provide charcoal, together with plantations and rice paddies, the products of a burgeoning human population. The final chapter, The Lost World, describes the adventures of Beehler and his group in a high mountain camp in a pristine area of the Foja Mountains in Paupa (Irian Jaya) in 2005. After arriving by helicopter, they surveyed the plants and animals and resolved long-standing mysteries regarding a bird of paradise, a bowerbird, and a tree-kangaroo.

The book is about adventure, marvelous birds and mammals, and the trials and tribulations of conservation of rainforest in developing countries. In the Epilogue, Beehler reiterates what he learned about conservation in each of his forays into the rainforests of the planet and concludes with the statement: "We conservationists have to insure that all threads tie together: good governance, sensible economics, strong planning, enforcement, engaged local stewardship and, yes, creation and management of protected areas to preserve the most precious places on earth." Despite the bewildering conservation and bureaucratic problems the author has encountered, the book has a tone of guarded optimism.

The book is attractive with each chapter beginning with a black-and-white painting. The maps place you in the various rainforests and the photographs illustrate important people, places, and habitats. The book is directed at a general readership: only common names are given for organisms—a single-page appendix with scientific names would have been useful—and the bibliography (no in-text citations) contains only 35 entries. Nevertheless, the book contains much for the professional ornithologist and conservationist. The stories are well-written and sparkle with adventure. I recommend this delightful well-written book to anyone with an interest in rainforest birds or the conservation of rainforest ecosystems.—WILLIAM E. DAVIS JR., Professor Emeritus, Boston University, 23 Knollwood Drive, East Falmouth, MA 02536, USA; e-mail: wedavis@bu.edu

BIRDS OF THE DOMINICAN REPUBLIC AND HAITI. By Steven Latta, Christopher Rimmer, Allan Keith, James Wiley, Herbert Raffaele, Kent McFarland, and Eladio Fernandez. Barry Kent MacKay, Tracy Pedersen, and Kristin Williams, principal illustrators. Princeton University Press, Princeton, New Jersey, USA. 2006: vii + 258 pages, 57 color plates, 2 detailed maps, 1 line drawing, and numerous range maps. ISBN: 978-0-691-11890-1, $75.00 (cloth). ISBN 978-0-691-11891-8 $35 (paper).—Mention the Dominican Republic (DR) to most Americans and they think of Albert Pujols or any number of excellent baseball players from that tiny country. To the knowledgeable tropical birder, though, thoughts of the DR immediately bring to mind 31 endemic species and literally dozens of endemic subspecies found on that island. Among the endemics are such unusual forms as Palmchat (*Dulus dominicus*), Least Parauque (*Siphonorhis brewsteri*), and Bay-breasted Cuckoo (*Coccyzus rufigularis*), plus an assortment of ground-tanagers, palm-tanagers, chat-tanagers, todies, and crows. Fortunately, most of these species are still reasonably common and can be found in the many new national parks and preserves that have been developed in the DR in recent years. Although a budding ecotourism industry catering to birders has developed in recent years, the Dominican Republic still seems fairly safe for an independent traveler who can speak a little Spanish (albeit Spanish that seems to function without the letter s). With this new field guide and a good map, he or she has a chance to see a majority of these island endemics in a short period of time.

This field guide begins with an introduction to the island of Hispaniola, which supports the countries of the Dominican Republic and Haiti. We learn this is an interesting place with what is now a single island having been split in two at various times in the past. This helps explain some of the rather unusual distributional patterns of some of the endemic birds, where new species evolved on the separate islands and either stayed in place, with ecologically equivalent species having ranges on what effectively were the two separate islands, or spread across the island, allowing two similar species to occupy most of the island but separate ecologically in some fashion (as in the two todies). The many endemic species and subspecies are listed and discussed. A section covers the advances made in conservation on this island in recent years with a list of the mostly new national parks. The problems facing these parks and birds outside of protected areas are also presented.

A series of 57 color plates fills the second section of the book. Most of these plates were copied from those used in *A Guide to the Birds of the West Indies* by Herbert Raffaele and others. Because Raffaele developed his book as part of his job in the federal government, he has been able to let ornithologists from other West Indian islands use parts of this material for developing regional bird books. Latta et al. took good advantage of this fact, although they also added 105 new images of Hispaniolan birds in this section. These plates do a wonderful job of illustrating the West Indian endemics and provide some images of the many winter residents on this island; one may still want to bring along a field guide from home to deal with more unusual plumages among these winter residents.

The bulk of the book (~200 pages) covers species descriptions, with usually about two species per page. Most species have a map of the island that shows their distribution, although that is also described in the text in more detail. Much of the distributional material comes from the annotated checklist of Allan Keith and collaborators: *The Birds of Hispaniola: Haiti and the Dominican Republic.* These species accounts are quite complete, and often provide some natural history of the species involved. Common names for each species in both the DR and Haiti are provided.

Appendix A has nine pages of detailed descriptions of birding sites in both countries. Appendix B provides a checklist. Two indices are provided, one with local names and one with scientific and common names. A list of references ends the book.

Although I reviewed only the English version of *Birds of the Dominican Republic and Haiti*, both French and Spanish versions of this book were produced at the same time as the English version. This was possible, in part, because of the reduced investment in color plates. The Dominican Republic has made admirable strides in recent years with regard to conserving natural resources such as birds

through developing reserves and changing laws. Having a book that is written in your language and about your birds can be an important rallying point for local biologists, as they deal with the local poverty and lack of federal support for their efforts. For this reason alone, the authors of this book are to be commended for producing such a fine regional work, as it undoubtedly will help preserve birds in the Dominican Republic in the future. Unfortunately, conditions are so environmentally devastated in Haiti that even a wonderful field guide written in French will probably do little to save birds there. That certainly is not the fault of this well written field guide.—JOHN FAABORG, University of Missouri, Columbia, MO 65211, USA. e-mail: faaborgj@missouri.edu

AVES BRASILEIRAS E PLANTAS QUE AS ATRAEM [BRAZILIAN BIRDS AND PLANTS THAT ATTRACT THEM]. By Johan Dalgas Frisch and Christian Dalgas Frisch. Dalgas Ecoltec, São Paulo, Brazil. 2005: 480 pages, 98 color photographs, 193 color plates, and 1254 maps. ISBN 85-85015-07-1. (cloth). AVES BRASILEIRAS: MINHA PAIXÃO (BRAZILIAN BIRDS: MY PASSION). By Johan Dalgas Frisch. Dalgas Ecoltec, São Paulo, Brazil. 2005: 186 pages, many color and black-and-white photographs. ISBN 85-85015-08-X. (cloth). $49.00 for both books plus postage (from www.avesbrasileiras.com.br).—The first of these two books, both of which are virtually entirely in Portuguese and come as part of a single-price package, represents the third edition of a guide first launched in 1981. In its current incarnation it purports to provide an accurate field guide to Brazilian birds (the bulk of the book), but also to provide an illustrated manual to what would be termed in the U.K. as "gardening for wildlife". To this end, the father and son Frisch team devote just fewer than 60 pages to explaining how to attract wild birds to your Brazilian garden, should you be fortunate to possess one (most Brazilians don't, even amongst the expanding middle classes), by planting certain trees and shrubs. Other chapters of this unconventional field guide are devoted to the national bird concept (Frisch senior was instrumental in Brazil's adoption of the Rufous-bellied Thrush (*Turdus rufiventris*) as the country's national bird), unraveling the mysteries of migration, nature's influence on poets and writers, the history of the present work, and the importance of creating habitat for birds and, by extension, other wildlife. Naturally, most readers of this review will be interested in how this book might serve them as a guide to identifying Brazilian birds.

It is claimed that the field guide follows the latest thinking on avian classification, although the systematics used are, in fact, those of Sibley and Monroe, which were certainly ground-breaking at the time (1990), but in today's fast-moving world of "molecular ornithology" look somewhat dated. The authors would have done better to have followed the list published online by the Brazilian Comitê Brasileiro de Registros Ornitológicos (http://www.cbro.org.br), which is constantly updated to reflect novel developments in nomenclature and taxonomy, as well as on the basis of new records, or if they preferred a book format list, that presented in the third edition of Howard and Moore (E. C. Dickinson. [Editor]. 2003. *The Howard and Moore Complete Checklist of the Birds of the World*. Christopher Helm, London, UK).

The material is arranged with text and maps facing the illustrations of the relevant species in "true" field guide format. The text, however, is minimal, providing merely the Brazilian, English, scientific, and Spanish names, as well as each species' total length with, at the foot of each page, an explanation of the etymology of the scientific name (in Portuguese). Identification features, habitat, vocalizations, etc., are all left to the imagination. It might also be added that in some particularly "busy" double-page spreads, for instance the 21 species of Tyrannidae packed onto pages 234–235, the relevant etymology section appears elsewhere, in this example on page 62! The maps are clear and well produced, albeit at a scale that will never permit detailed elucidation of range, and seem comparatively free of dramatic errors, although needless to say in a work of this scope there are some. They also endeavor to portray range throughout South America, not just in Brazil.

This book contains >3,000 individual images. Despite this number, a great many dis-

tinctive female (and other) plumages are not illustrated and, even worse (perhaps especially from the point of view of the visiting birder), well over 500 species that have occurred in Brazil, including several distinctive or exciting endemics, are not even mentioned, much less depicted. (Although the authors mention the approximate number of species (1,800) to have occurred in Brazil in their introduction, the number omitted from this book seems to be nowhere admitted.) As a result, keen visitors eager to add such sought-after species as Black-hooded Antwren (*Formicivora erythronotos*), Restinga Antwren (*F. littoralis*), or Marsh Antwren (*Stymphalornis acutirostris*), to name just three Thamnophilidae, will be unable to identify them using this book. As further examples, most species of Laridae, and a great many shorebirds and pelagic birds are all left undepicted. Although the introduction to the new edition does not clearly state at whom the book is directed, the emphasis is presumably on the amateur Brazilian (of which it might be stated there are still very few who specifically travel to watch birds purely as a hobby), but even then the choice of species is still confusing. One might just understand the rationale for including Spix's Macaw (*Cyanopstitta spixii*), although it should have been coupled with a note concerning its extinction in the wild, but why illustrate Eskimo Curlew (*Numenius borealis*), which judging from the map might still be expected just about anywhere in southern and western South America! It goes without saying that in the unlikely event the person fortunate enough to re-encounter the near-mythical Kinglet Calyptura (*Calyptura cristata*) is reliant on this book; they will not find it herein.

The illustrations themselves sadly leave much to be desired. The same attenuated profile appears to have been used as a basis for every raptor, and a similar "color by numbers" charge can be leveled at other groups too. Bill shapes are often at significant odds with reality, colors frequently range from far too gaudy (most tinamous and pigeons, for example) to the opposite extreme, and all species are shown perched, even seabirds, swifts, and hirundines. It should be remarked that the observer familiar with Brazilian, or South American birds, will still be able to identify a great many of the more boldly marked species (e.g., tanagers) using this book, but the beautifully intricate plumages displayed by many woodcreepers, nightjars, and owls appear almost monstrous as depicted here. Some images do stand out as being much better than the remainder, including all those associated with the "gardening for wildlife" section, and some of the toucanets, for example, within the field guide section, presumably because they were painted by a different artist, apparently Tomas Sigrist, based on the style, although his name does not appear to be credited.

With the recent publication of the long-awaited *Birds of Peru* (Schulenberg et al. 2007. Princeton University Press, Princeton, NJ, USA), birders traveling to South America particularly await modern field guides for Brazil and Bolivia. Fortunately, several for the former country are in production, so that just like the "from rags to riches" tale that has unfolded for those birding the Indian Subcontinent in recent years, we may in the future witness a situation where the birder is faced not with the challenge of finding a reliable book to carry in the field, but deciding which book to take. That time is not yet come, but in the interim, there are two better field guides to Brazilian birds than the one reviewed here. *All the Birds of Brazil* (*Todas as Aves do Brasil*) by Deodato Souza (2006. Subbuteo Natural History Books, Shrewsbury, UK) has been on the market for some years, in both English and Portuguese editions. The illustrations are small and frequently poor, but the brief text frequently covers vocalizations, mainly cribbed from Sick, Ridgely and Tudor, or other reliable sources. More recently published is Tomas Sigrist's dual-language field guide (2007. *Birds of Eastern Brazil/Aves do Brazil Oriental*, São Paulo, Brazil), which boasts superior illustrations to any other Brazilian field guide. Indeed, some of the plates, including many raptors and antbirds, by Eduardo Brettas are of the same standard as those adorning major North American or European field guides. Unfortunately, Sigrist's work solely relies on a key to impart information concerning habitat and distribution, and there is nothing on vocals or hints on identification, despite their being quite considerable white space left unused on most pages facing the plates. Both these latter works are

less bulky and more accurate than that by the Frisch team.

The second part of the present package is a book, entirely in Portuguese, subtitled the life and work of Johan Dalgas Frisch, and this recounts his efforts at recording Brazilian bird song, campaigning for the implementation and protection of Tumucumaque National Park on the Brazilian frontier with French Guiana and Suriname, and documenting the migration of U.S.-breeding Purple Martins (*Progne subis*) to and from the State of São Paulo, in southeast Brazil, amongst other subjects. Frisch has plainly understood the imperative of interesting and gaining the support of the rich and powerful, if one is to succeed in conservation work, as numerous photographs in the book prove. Given the large number of environmental challenges facing Brazil, more characters like Frisch with the capacity to popularize birds and other wildlife, will be needed. Also of importance, as has been demonstrated elsewhere in the world, is the production of an accurate, cheaply priced, and appropriately sized field guide to the country's birds in the native language, to engender a large-scale interest in birds, and their conservation, among the general public.—GUY M. KIRWAN, 74 Waddington Street, Norwich NR2 4JS, UK; e-mail: GMKirwan@aol.com

CODING AND REDUNDANCY: MAN-MADE AND ANIMAL-EVOLVED SIGNALS. By Jack P. Hailman. Harvard University Press, Cambridge, Massachusetts, USA. 2008: xiii and 257 pages, 25 figures, 333 references. ISBN 978-0-674-02795-4. $39.95 (cloth).—The introduction reviews the history of ideas in animal behavior, communication, and its coding. The other chapters describe the principles of behavior codes. Analogies are used to match cases of human signals in man-made machines and animal signals with many examples for birds, several from studies by the author.

The chapters describe many levels of complexity of signals with examples for each level. How are headlight-taillight colors of cars like gender plumage markers in woodpeckers; weather radio alarm calls like bird nest-departure calls; indicator lights on waffle irons like wing-flagging in copulating gulls; or a smoke-detector test like a Herring Gull (*Larus argentatus*) parent and chick in begging for food? Answers: these are cases of binary coding, where one signal has two states: the first, simple one-bit signals (flicker male and female); the second, event markers when the signal is on briefly when the status changes; the third, state indicators (signal is on while a state is maintained); the fourth, status replies where a check by one individual either elicits a signal in response or gets no response (if chick pecks at red spot on parent's bill, then parent regurgitates food).

Other classes of signals involve more than two states ("multi-valued coding") and more than two kinds of signals ("multivariate coding"). For a man-made signal, the author describes the Morse code. Samuel Morse invented telegraphy and the code that made it a useful means of communication in the early 1800s. A sender presses a key to close an electric circuit, releases the key to open the circuit; this sends a signal each time the key is pressed and each time it is released. Each letter is composed of clicks with short intervals, or long intervals, or a mix of short and long intervals between them. In English, the most frequently used letter was E (13% of the letters), next T, next A and O, then I, N, R; and the least used letters were Q and Z (less than 1%). Morse assigned shorter signals for frequently used letters and longer signals for less frequent letters. His code included the time between clicks within a letter (short or long), between letters (a longer time), and the frequency of use of the letters in his signal design. A single short click (. or dot) was used for E, a long click (– or dash) was used for T, three short clicks for S (. . .), a short click and then a long click for "A" (.–), and so on. The code is designed for efficiency in time of signal transmission, as it takes less time to code and transmit a common letter than a less common letter.

In a bird signal, the Black-capped Chickadee (*Poecile attricapillus*) "chick-a-dee" phrase in the presence of a predator has more "dee" notes when the predator is small than when it is large. This makes sense in terms of "design", as small predators (such as a small owl) are more likely to attack a chickadee than large predators (a large hawk), so the higher

number of "dee" notes per call is more likely to signal imminent danger to the social partners of the calling chickadee. Both Morse code and chickadee alarm calls are cases of multi-valued coding.

Other signals are multivariate, either discrete or composite. A man-made example is Braille, a discrete linguistic code used by the blind and detected by touch. The code involves the presence or absence of raised dots in three rows of dots in two columns, where the combination of raised dots codes a letter. The code consists of six on/off variables, so a composite signal can have two (exp 6) = 64 different values, which represent letters and numerals and other things.

A bird example is the pattern and color of duck wings. In eastern North America, each species of dabbling duck has a unique composite visual signal. The author recognizes eight colors that occur in different combinations on seven parts of the wing. The seven spatial elements are like seven code words, and each patch can have one of the eight colors. These signals may let the ducks sort into single-species flocks when a mixed group takes flight. We do not know that ducks sort this way, or that there is an adaptive value to be in several small flocks rather than a large mixed flock, but the potential information is there.

A novel approach of the book is the application of information theory to a wide range of signaling systems in humans and animals such as birds. Hailman explains how to estimate the *information* in signals. The text and an appendix use the terms and equations to estimate the parameters of *information* ($H = \log_2 n$); *entropy*; *surprisal* ($S = \log_2 p$), or "news", as in "when a dog bites a man that is not news, but when a man bites a dog that is news"; and *redundancy* of simple and complex signal coding. However, not much use is made of these parameters, and the "information" from the signal sender is not always used by the receiver. Not all states are equally likely, and this can be taken into account in describing the information in binary coding. The estimates are not used to predict differences between species. Nor are the information-theory parameters compared across different classes of signals (such as kinds of behavior). The author explains the coding of the ISBN number of the book as an error-checking case of "designed redundancy". He advises the math can be skipped when reading the book.

The book is clearly written and a fascinating read, as well as informative and interesting. It shows ordinary readers as well as biologists how to recognize connections between the design of codes and behavior signals, and to see the great variety in animal signals, in many behaviors and many kinds of birds.—ROBERT B. PAYNE, Professor Emeritus, University of Michigan, 1306 Granger Avenue, Ann Arbor, MI 48109, USA; e-mail: rbpayne@umich.edu

The Wilson Journal of Ornithology 120(4):927–940, 2008

PROCEEDINGS OF THE EIGHTY-NINTH ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The eighty-ninth annual meeting of the Wilson Ornithological Society (WOS) was held Thursday 17 April, through Sunday, 20 April 2008 at the Mobile Convention Center, Mobile, Alabama in joint session with the Association of Field Ornithologists (AFO), at the invitation of the University of Southern Mississippi (USM) Migratory Bird Research Group and sponsored by the Gulf Coast Bird Observatory, Mississippi Coast Audubon Society, University of Southern Mississippi, Dauphin Island Sea Laboratory, University of California Press, USM Coastal Research and Extension Center, and the Grand Bay National Estuarine Research Reserve (NERR). Frank R. Moore, Director of the USM Migratory Bird Research Group, chaired the local committee, which also included Robert Diehl, John Dindo, Jennifer Owen, and Mark Woodrey.

The WOS Council met from 1307 to 1802 hrs on Thursday, 17 April, in Room 105-B of the Mobile Convention Center. That evening there was a social at the Center for the conferees and guests. The Council met again from 1121 to 1306 hrs the following day.

The opening session on Friday convened in a large space at the Center known as Room 210-BCD at 0806 hrs with welcoming remarks from Frank R. Moore, WOS President James D. Rising, and AFO President Cecilia M. Riley. Timothy J. O'Connell, Chair of the WOS Student Travel Awards Committee, offered comments on those awards, and Mark Woodrey of the local committee provided information concerning field trips. The opening ceremony continued with a presentation by Edward H. Burtt Jr. on Margaret Morse Nice, which led to his introduction of Jerome A. Jackson, who concluded the opening ceremony by delivering the Margaret Morse Nice Plenary Lecture, "Thinking like a mountain, seeing like a woodpecker: behavioral ecology and conservation of woodpeckers."

The scientific program included 58 contributed papers and 47 contributed posters, which were organized into eight paper sessions, a poster session, and a symposium on migration and coastal ecology. In addition, WOS hosted the Margaret Morse Nice Lecture, and the Association of Field Ornithologists hosted the AFO Plenary Lecture, "How phylogenies can guide research in other fields: examples from hummingbirds," presented by J. Van Remsen. On Friday evening the poster session was held in conjunction with a reception at the Center.

In addition to self-guided bird-watching opportunities in the vicinity of the Mobile Convention Center, the local committee organized several longer field trips. These included two trips each to Dauphin Island and the Pascagoula River, and a post-conference trip to Grand River National Estuarine Research Reserve.

The conferees enjoyed a 60-min reception prior to the annual banquet, which was held in a very large space at the Center known as Room 201-ABCD. After an enjoyable dinner, WOS President James D. Rising introduced the new AFO president, David N. Bonter. President Bonter led those assembled in an expression of gratitude to Frank R. Moore, Chair of the local committee, and the many persons who had worked hard to make the conference a success; this expression took the form of a collective bout of exuberant hand clapping. After presenting AFO awards, President Bonter returned the podium to WOS President Rising, who in turn thanked the three elected members of the WOS Council who had completed their terms of office, Robert L. Curry, Daniel Klem Jr., and Douglas W. White, and welcomed the three newly elected members of Council, Jameson F. Chace, Sara R. Morris, and Margaret A. Voss. The following WOS awards and commendations also were presented:

MARGARET MORSE NICE MEDAL
(for the WOS plenary lecture)

Jerome A. Jackson, "Thinking like a mountain, seeing like a woodpecker: behavioral ecology and conservation of woodpeckers."

EDWARD'S PRIZE
(for the best major article in volume 119 of *The Wilson Journal of Ornithology*)

James A. Cox and Gary L. Slater, "Cooperative breeding in the Brown-headed Nuthatch."

WILLIAM AND NANCY KLAMM SERVICE AWARD
(for distinguished service to the Wilson Ornithological Society)

Richard C. Banks.

LOUIS AGASSIZ FUERTES AWARD

Andrés Cuervo, "The evolutionary assembly of a species rich avifauna: avian speciation and differentiation in the Andean cloud forest."

PAUL A. STEWART AWARDS

Anya Illes, "Do female Stripe-headed Sparrows outsing their mates during territorial incursions?"

Irene Liu, "Female eavesdropping and male song type matching in a songbird."

Trina Schneider-Bayard, "Quantifying cues: testing the influence of social cues on habitat selection behavior."

Andrea Townsend, "Optimal dynamics of sociality, relatedness, and parasites in American Crows: linking theoretical predictions with empirical data."

ALEXANDER WILSON PRIZE
(for best student paper)

Curtis W. Budney, "Comparative phylogeography of neotropical birds: ecology predicts levels of genetic differentiation."

LYNDS JONES PRIZE
(for best student poster presentation)

Zoltán Németh, "Phenotypic organ flexibility around the annual cycle in two Nearctic-neotropical migratory thrush species."

NANCY KLAMM BEST UNDERGRADUATE STUDENT ORAL PAPER AWARD

Kelly Hallinger, "Lifetime fitness of Tree Swallows exposed to aquatic mercury."

NANCY KLAMM BEST UNDERGRADUATE STUDENT POSTER AWARD

Jack M. Stenger, "The bacterial degradation of phaeomelanic and eumelanic feathers."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

Eric Beck, Cameron University, "Oklahoma marshbird monitoring project."

Bethany Belock, Saint Mary's College, "An example of the role of weight, plumage color, cere color, and total area of UV reflectant plumage on mate selection in Budgerigars (*Melopsittacus undulates*)."

Peggy Buckley, Canisius College, "A comparison of migrant species composition at two western New York television towers."

Ryan Burdge, College of William and Mary, "Avian pesticide exposure and food intake on golf courses."

Curtis Burney, Louisiana State University, "Comparative phylogeography of neotropical birds: ecology predicts levels of genetic differentiation."

Vince Cavalieri, Oklahoma State University, "Scale effects on occurrence and relative abundance of forest songbirds in eastern Oklahoma."

Katie Chmielowiec, Canisius College, "A comparison of fall migration and stopover by Northern Saw-whet Owls during irruptive and nonirruptive years in coastal Maryland."

Charles Clarkson, University of Virginia, "Food supplementation, territory establishment, and song in the Prothonotary Warbler."

Jason Courter, Eastern Kentucky University, "Responses of flocks of Tufted Titmice to different-sized raptors."

Katherina Forgues, Trent University, "Making the connection between shorebirds and off-road vehicles."

Maura Hanna, Canisius College, "Morphological differences in Gray Catbirds across age classes."

Bruce Hitch, Auburn University, "Do avian abundances differ between habitat types? Implications for assessment of habitat quality."

Ian Horn, Eastern Kentucky University, "Eastern Phoebes use different strategies to provision young."

Mikaela Howie, College of William and Mary, "The infiltration of aquatic mercury into a terrestrial ecosystem."

Jason Jacobs, Canisius College, "Seasonal differences in energetic condition of Blackpoll Warblers on Appledore Island."

Erik Johnson, Louisiana State University,

"Ectoparasites affect bird condition in neotropical forest fragments."

Christine Lattin, Eastern Kentucky University, "Is song length an important signal of aggression for Blue Grosbeaks? A playback experiment."

Kristen Lear, Ohio Wesleyan University, "Bacterial degradation of flight and body contour feathers by *B. licheniformis*."

Kim Martinczack, Saint Mary's College, "Relationships between dominance measures and physical characteristics of the Budgerigar (*Melopsittacus undulates*)."

Damion Marx (deceased), Florida Atlantic University, "Relationships among peak annual wading bird nest effort, lake stage, and hydrologic recession at Lake Okeechobee, Florida, USA."

Emily Runnells, Hobart and William Smith, "Fat stores and energetic condition of *Catharus* thrushes during spring and autumn migration at a Great Lakes stopover site."

Stacy Stefan, College of Charleston, "Seasonal variations in recoveries of South Carolina-banded Brown Pelicans and Royal Terns: a comparison of two seabird species experiencing a decline in local nesting numbers."

Jack Stenger, Ohio Wesleyan University, "The bacterial degradation of phaeomelanic and eumelanic feathers."

Bethany Stephan, Canisius College, "Comparison of avifauna in three riparian environments in western New York: the impact of anthropogenic habitat alteration."

Amanda Stockwell, Canisius College, "Migration and stopover ecology of the Tennessee Warbler at an inland stopover site near Kalamazoo, Michigan."

Ryanne Sullivan, Canisius College, "Annual variation in the stopover ecology of the Tennessee Warbler in Michigan."

Sean Williams, Ohio Wesleyan University, "Structure of albino feathers: why so weak?"

Meredith Wilson, Ohio Wesleyan University, "Dynamics of *Staphylococcus aureus* on bird feathers."

Selection committee for the Nice Medal: Doris J. Watt (chair), Charles R. Blem, William E. Davis Jr.; for the Edwards Prize: Clait E. Braun (chair), J. Daniel Lambert, Cynthia A. Stacier; for the Klamm Service Award: Sara R. Morris (chair), William E. Davis Jr., Jerome A. Jackson, John C. Kricher, Doris J. Watt; for the Fuertes and Stewart Awards: Robert B. Payne (chair), Laura Payne; for the Alexander Wilson Prize, the Lynds Jones Prize, and the Nancy Klamm undergraduate presentation awards: E. Dale Kennedy (chair), Mary Bomberger Brown, L. Scott Johnson, Daniel Klem Jr., Alan Maccarone, John A. Smallwood, Margaret A. Voss, Douglas W. White; and for the WOS Travel Awards: Timothy O'Connell (chair), David Bonter, Mia R. Revels.

BUSINESS MEETING

President James D. Rising called the annual WOS Business Meeting to order at 1731 hrs, Friday, 18 April 2008, in Room 201-BCD in the Convention Center and recognized that a quorum was present. Secretary John A. Smallwood presented a synopsis of the previous day's Council meeting, noting that at the end of March 2008, the society's membership stood at 1,690 individuals, including 211 students and 84 new members of all membership categories; the renewal rate for previous members was 82% for the current year. In addition, 319 libraries and institutions subscribed to *The Wilson Journal of Ornithology*. The Secretary then asked those gathered to stand in recognition of the following members who had died since the last annual meeting: W. Marvin Davis (University, MS), George A. Hall (Morgantown, WV), Frederick E. Ludwig (Barbeau, MI), Franklin McCamey (Decatur, GA), Val Nolin (Bloomington, IN), Kenneth C. Parkes (Pittsburgh, PA), Henry W. Pelzel (Wichita, KS), Darrell W. Pogue (Tyler, TX), R. M. Schramm (Tucson, AZ), Henry T. Wiggin (Brookline, MA), Glen E. Woolfenden (Venus, FL), and Addison Young (Larchmont, NY).

Secretary John A. Smallwood then remarked to those assembled that encouraging students to participate in our meetings and to make presentations in the scientific programs is a high priority of the Wilson Ornithological Society. Because this was a joint meeting with AFO, the two societies pooled their funds allocated for student travel awards. All 39 students who applied for travel funds submitted applications that were deemed worthy of some level of financial support. Because there were so many students and the cost of travel had become so high, the amount of aid requested

was significantly greater than the $9,000 allocated for travel awards. Secretary Smallwood was pleased to report that WOS Council had allocated an additional $3,600 in travel support for those students participating in this meeting.

Secretary John A. Smallwood informed those assembled that Council had unanimously re-elected Clait E. Braun as Editor of *The Wilson Journal of Ornithology* for 2009, and noted that under Editor Braun's care the Journal sets a high standard for peer-reviewed publication.

Finally, the Secretary expressed WOS Council's gratitude to the Investing Trustees for their superb management of the society's investments, especially during the current period of widespread economic uncertainty. Having completed his synopsis of the Council meeting, Secretary Smallwood first introduced Treasurer Melinda M. Clark, who presented the Treasurer's Report, and then Editor Clait E. Braun, who presented the Editor's report.

John A. Smallwood, as Chair of the Nominating Committee, which also included Mary Bomberger Brown, Edward H. Burtt Jr., and Douglas W. White, presented that committee's report: Members of Council for 2008–2011 (3 nominees for 3 positions), Jameson F. Chase, Salve Regina University; Sara R. Morris, Canisius College; and Margaret A. Voss, Pennsylvania State University-Erie. Those assembled were invited to make additional nominations, but no one did so. Thus, President James D. Rising closed the nominations as a result of a motion by Dale Kennedy, seconded by Reed Bowman; that motion was passed unanimously by voice vote. Jerry Jackson then moved and Dan Klem seconded that the Secretary cast a single unanimous vote for the slate of nominees, and by acclamation, it happened that way.

Having come to the end of the WOS Business Meeting agenda, President James D. Rising inquired if any of those assembled had additional items of business. Because no one offered any, Sara Morris moved and Bob Beason seconded that the meeting stand adjourned. This came to pass at 1643 hrs.

REPORT OF THE TREASURER

Statement of Revenues and Expenses For The Year Ending 31 December 2007

	2007 12 Months Actual	2007 Annual Budget	2008 Annual Budget
Revenues			
Contributions	$ 1,836	$ 1,200	$ 1,200
Student Travel Research Fund	315	—	—
Van Tyne Library Book Fund	86	—	—
Sales—back issues	239	518	518
Sales—books—Van Tyne Libr.	609	500	500
Subscriptions	15,070	17,317	17,317
Page charges	18,390	15,506	15,506
Royalties	4,230	3,409	3,409
BioOne Electronic Licensing	13,469	10,760	10,760
Mailing list rental income	222	660	660
Memberships	26,767	31,332	31,332
Other income	3,625	—	—
Total revenues from operations	**$ 84,858**	**$ 81,202**	**$ 81,202**
Expenses			
Journal publication costs			
Editorial honorarium	$ 8,000	$ 4,000	$ 4,000
Editor travel/supplies	6,474	1,000	1,000
Editorial assistance	17,291	25,000	25,000
Copyright expense		48	48
Printing—bulletin	71,645	64,400	64,400
Artwork	900	—	—
Printing color plates	1,125	2,400	2,400
	$ 105,435	$ 96,848	$ 96,848

Operating expenses			
Postage & mailing—back issue	$ —	$ 440	$ 440
Storage back issues	301	680	680
Van Tyne Library—expenses	710	1,500	1,500
OSNA management services	24,221	21,000	21,000
Credit card fees	1,150	1,100	1,100
Travel expenses—OSNA rep		1,500	1,500
Travel expenses—general	788	450	450
Travel expenses—Ornith Council	242	200	200
Meeting expenses	3,747	1,000	1,000
Membership expenses	1,377		2,000
Accounting fees	2,283	4,500	4,500
Insurance—D&O	1,650	1,425	1,425
Office supplies	498	570	570
Postage—general	169	260	260
Other expenses	154	—	35
Filing fees	5	5	5
Discretionary expenses		3,000	3,000
	$ 37,295	$ 37,630	$ 39,665
Awards			
Membership awards	$	$	$ 600
Hall/Mayfield	—	1,000	1,000
Stewart	2,500	3,000	3,000
Fuertes	2,500	2,500	2,500
Wilson, Lynds Jones, Klamm	1,400	1,200	1,200
Student travel grants	5,125	5,000	5,000
Nice award expenses	2,307	3,000	3,000
	$ 13,832	$ 15,700	$ 16,300
Contributions			
Support—Ornith Council	$ 9,000	$ 9,000	$ 9,000
Support—Ornith Council, restricted to revision costs	7,500	7,500	—
Am Bird Conservancy Dues	—	250	250
AAZN dues	—	250	250
	$ 16,500	$ 17,000	$ 9,500
Total Expenses	**$ 173,062**	**$ 167,178**	**$ 162,313**
Expenses in excess of revenues before investment	**$ (88,204)**	**$ (85,976)**	**$ (81,111)**
Investment activity			
Revenues			
Investment earnings—budgeted	$ —	$ —	$ —
Realized gain/loss—ML	35,219	23,612	23,612
Realized gains/losses—Howland	84,951	18,968	18,968
Realized gains/losses—Sutton	5,329	5,812	5,812
Unrealized gain/loss—ML	21,330	36,722	36,722
Unrealized gain/loss—Howland	(40,050)	29,887	29,887
Unrealized gain/loss—Sutton	9,761	4,794	4,794
Investment earnings—ML	26,981	20,000	20,000
Investment earnings—Howland	63,028	25,000	25,000
Investment earnings—Sutton	3,914	4,200	4,200
Total revenues from investment activity	**$ 210,463**	**$ 168,995**	**$ 168,995**
Investment fees	**$ 28,461**	**$ 25,091**	**$ 25,091**
Investment revenues in excess of expenses	**$ 182,002**	**$ 143,904**	**$ 143,904**
Total revenues in excess of expenses	**$ 93,798**	**$ 57,928**	**$ 62,793**

STATEMENT OF FINANCIAL POSITION

31 December 2007

Assets		
Cash investments		
Merrill Lynch—cash	$ 46,791	
Coamerica—Van Tyne checking	1,543	
Van Tyne Univ Michigan account	434	
Sutton Fund—cash equivalents	12,947	
Howland Mgmt—cash equivalent	229,775	
Total cash and cash equivalents		$ 291,490
Other Investments		
Merrill Lynch—common stocks	766,559	
Merrill Lynch—corp bonds	37,990	
Merrill Lynch—mutual funds	47,711	
Sutton Fund—equities	155,437	
Sutton Fund—corp bonds	9,303	
Howland Mgmt—equities	1,326,209	
Howland Mgmt—fixed income	246,918	
Total Other Investments		2,590,127
Total Assets		$ 2,881,617
Fund Balances		
Restricted funds—Sutton Fund	$ 177,686	
Unrestricted funds	807,231	
Net Income	93,798	
	901,029	
Fund balance–Klamm	1,802,902	
Total Fund Balances		$ 2,881,617

Melinda M. Clark, *Treasurer*

EDITOR'S REPORT

This report is for the period 1 January through 31 December 2007. We received 190 new manuscripts in 2007. Only one of these manuscripts was published in Volume 119 (2007), illustrating the backlog of manuscripts from 2006 and earlier. However, 9 received in 2007 are in the March 2008 (Volume 120) Issue and 23 will be in the June 2008 Issue (already sent to Allen Press). All four Issues of Volume 119 were published on schedule in 2007 and we expect this pattern will continue. We are slowly trying to increase the rejected and withdrawal rates but need stronger reviews to help encourage authors to send their manuscripts to other possible outlets.

We have made up the September 2008 Issue (31 manuscripts) and presently have 38 additional accepted manuscripts awaiting publication. This number will more than fill the December 2008 Issue and it is unlikely that any manuscripts received in 2008 will be published in 2008. Thus, we continue to have a backlog even though we published 826 pages (119 papers) in 2007. I do note that both *Condor* (1,000) and *Auk* (1,500) publish more pages each year. There is a cost for publishing more pages as cost per page is ~$100.

The number of manuscripts received from outside of North America (north of Mexico) is increasing and is expected to increase markedly in the future. *The Wilson Journal of Ornithology* is seen as a desirable publication outlet, especially by authors trained in North America and now working in Mexico and South America. We published 24 papers in 2007 by authors outside of North America (14 from Mexico and South America). Locations of the senior authors of non-Central or South America manuscripts ranged from China to Israel to New Zealand. We published an additional 13 manuscripts by authors in North America on studies completed on species out-

side of North America. We truly are attracting an international audience as we publish more papers from outside of North America. We have added one person to our editorial board to help with manuscripts from Mexico and South America. All manuscripts by authors whose first language is not English take considerable effort from the editorial office.

We continue to use electronic and paper mail, and all reviewers are contacted by e-mail. Authors in North America are requested to submit one paper copy and an electronic file. Authors from outside of North America can use electronic submission at their discretion. The process is functional and can be speedy, depending largely on referees and authors promptly returning manuscripts to us.

The past 18+ months have convinced me that editing a major journal is not a part-time "job" as one could spend most of his or her time working on editorial matters. Both the Editor and Editorial Assistant could be full time positions.

I look forward to continuing to serve the Wilson Ornithological Society.

Clait E. Braun, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

The Wilson Ornithological Society is welcoming and generous to undergraduate students. We hope our efforts will through time sustain an active society membership. Presenting a poster or paper at a national ornithological meeting is a landmark experience for an undergraduate student. In addition to discounted membership dues, we also offer support for participation in meetings, including travel funds, free one-year memberships, banquet tickets, and awards for paper and poster presentations. Young students are now a major feature at our annual meetings; more than half of the presentations on the program for the Mobile meeting are by undergraduate and graduate students.

To maintain our attractiveness in the face of rising meeting costs and competition from sister societies, we should monitor our support levels. On-line discussions prior to the meeting have considered offering additional dollars for student travel to meetings. Expanded membership discounts to students are another possibility.

To assess how our undergraduate outreach is being received by the students themselves, I am working with the IT Department at Albion College to create an on-line forum to solicit suggestions from undergraduate and graduate student members on how the society could be of more use to them. My goal is to have this site up as soon as possible after the annual meeting. I welcome suggestions on topics for discussion threads.

Faculty mentors are the basis for our success in generating the level and quality of undergraduate participation in our meetings that we now enjoy. Consequently, encouraging mentoring faculty to be active in WOS could be our most effective outreach endeavor. The work of the Nominating Committee in identifying and recruiting mentoring professionals is important. Perhaps it would be useful to feature symposia, workshops, or panel discussions on mentoring undergraduates or teaching ornithology as part of future meetings.

Douglas W. White, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

I am pleased to submit this report of the activities at the Josselyn Van Tyne Memorial Library for the period 1 January through 31 December 2007.

Loans

Loans of library materials included 25 transactions to 21 members. These loans included books loaned, and copied and scanned articles.

Acquisitions

Exchanges: A total of 140 publications was received by exchange from 109 organizations or individuals.

Gifts: We received 29 publications from 25 organizations.

Subscriptions: We also received 30 publications from 22 subscriptions. We spent a total of $667 on subscriptions in 2007.

Donations: we received items from 6 members and friends: John Farmer, Lloyd Kiff (for

The Peregrine Fund) Phil Mattocks, Mike McLeish, Bob Payne, and Victor Zhukov, for a total of 257 items, including 27 books and 190 journal issues.

Purchases: 19 journal issues and 1 book, $110.50.

Dispersals

Gifts to Other Institutions: 163 issues of *American Birds* to the University of Windsor, 130 journal issues to the Peregrine Fund library, 5 books and 1 journal issue to the Archbold Biological Station library.

Back Issues: We sent out 33 back issues of *The Wilson Bulletin* for only the cost of postage.

Duplicates: We sold 16 books and 5 journal issues for $863.

Accessibility on the Web

Web Site: The web site (http://www.ummz.umich.edu/birds/wos/) continues to provide access to the library. Journals currently received are listed on the site as well as how to access the University of Michigan's on-line catalogue, which interested people can use to check holdings.

Books for Sale: We have our duplicate books for sale listed on the web site.

Journals for Trade: Also listed on the web site are the journals we have available for sale or trade.

Thank You's

Many thanks to our secretary, Janet Bell, for keeping the library loan records, and to our work-study student Rebecca Carter for copying and scanning articles, keeping the library running, and mailing out back issues of *The Wilson Bulletin/Journal.* Janet Hinshaw has done a wonderful job as the Wilson Ornithological Society Librarian. Thanks to our student library worker, Olivia Pennebaker, for copying and scanning articles, keeping the library running, and mailing out back issues of *The Wilson Bulletin/Journal.*

Robert B. Payne, *Chair*

REPORT OF THE SCIENTIFIC PROGRAM COMMITTEE

The Committee on the Scientific Program was chaired by WOS Second Vice-President Robert C. Beason and AFO First Vice-President David N. Bonter, who were assisted by session moderators Mark Deutschlander, Stephen Hager, Mikaela Howie, Austin Hughes, Karl Miller, Frank Moore, Scott Rush, Jean-Pierre Savard, and James Tucker.

PAPER SESSIONS

Migration and Coastal Ecology Symposium

Jeffrey Buler, University of Delaware and the USGS Wetlands Research Center, "Migratory birds and the changing coastal landscape."

Robb Diehl, University of Southern Mississippi, "Weather, migratory birds and the coastal setting."

Brent Hales, University of Southern Mississippi, "Coastal economic and social development."

Kim Hall, Michigan State University, "Global climate change impacts on coastal landscapes."

Paul Hamel, Hardwoods Experiment Station, USDA Forest Service, "Endangered/threatened migratory birds and the Gulf Coast."

Eben Paxton, USGS Southwest Biological Science Center, "Population regulation of migratory birds."

Mark Woodrey, Grand Bay NERR and Wylie Barrow, USGS Wetlands Research Center, and Bill Vermillion and Mark Parr, Gulf Coast Joint Venture, "Conservation of migratory birds along the Gulf Coast."

General Sessions

Arlene Arnold, Bart Ballard, and Thomas Langsheid, Texas A&M University, "Terrestrial habitat use and chronology of migrating birds through southern Texas."

John C. Arvin, Gulf Coast Bird Observatory, "Evidence of widespread northward range extensions along a 1000-km gradient from tropical to warm-temperate climates in northeastern Mexico and southern Texas."

Lisa Gardner Barillas and Yong Wang, Alabama A&M University, "Temporal and spatial variations of habitat associations of fall migrating songbirds at an inland site in northern Alabama, USA."

Charles R. Blem, Flathead Lake Biological Station, "Nest boxes and conservation of Prothonotary Warblers: a 21-year study."

David Bonter, Cornell Laboratory of Ornithology, "Eurasian Collared-doves in North

America: colonization dynamics and implications for native doves."

Peggy E. Buckley, Arthur R. Clark, and Sara R. Morris, Canisius College, "Comparison of migrant species composition at two western New York television towers."

Ryan B. Burdge and Daniel A. Cristol, The College of William and Mary, "Avian pesticide exposure and food intake on golf courses."

Curtis W. Burney and Robb T. Brumfield, Louisiana State University, "Comparative phylogeography of neotropical birds: ecology predicts levels of genetic differentiation."

John P. Carpenter, Yong Wang, and Hugh Metcalfe, Alabama A&M University, "Cerulean Warbler home range estimates and roost site selection in northeast Alabama."

Vincent S. Cavalieri, Timothy J. O'Connell, and David M. Leslie Jr., Oklahoma State University, "Scale effects on occurrence and relative abundance of forest songbirds in eastern Oklahoma."

Katie A. Chmielowiec, Canisius College, David Brinker, Maryland Department of Natural Resources, and H. David Sheets and Sara R. Morris, Canisius College, "A comparison of fall migration and stopover by Northern Saw-whet Owls during irruptive and nonirruptive years in coastal Maryland."

Charles Clarkson, University of Virginia, "Food supplementation, territory establishment, and song in the Prothonotary Warbler."

Robert L. Curry, Villanova University, "Contributions of George F. Gaumer to ornithology of the Yucatan and Cozumel: throwing the baby out with the bathwater?"

Anthony C. Dalisio, Sterling College, William E. Jensen, Emporia State University, and Timothy H. Parker, Whitman College. "The response of male Dickcissels to geographic song variation."

Mark Deutschlander, Hobart and William Smith Colleges, and Rachel Muheim, Virginia Polytechnic Institute, "Fuel reserves affect migratory orientation of thrushes and sparrows both before and after crossing an ecological barrier near their breeding grounds."

Robert C. Dobbs and Paul R. Martin, Queen's University, and Wylie C. Barrow Jr., and Clinton W. Jeske, USGS National Wetlands Research Center, "Hurricane-related declines in food availability and migrant land bird abundance at autumn stopover sites."

Ryan M. Dziedzic and Michael J. Hamas, Central Michigan University, "Spring stopover of forest-dwelling and shrub-dwelling migrants at a Great Lakes coastal wetland: the roles of habitat, arthropods, and phenology."

Megan J. Fitzpatrick, Douglas W. White, and E. Dale Kennedy, Albion College, "The effects of thermal environment on incubation behavior in House Wrens (*Troglodytes aedon*)."

Sarah E. Goodwin and W. Gregory Shriver, University of Delaware, "Declines of sound sensitive species in response to increased traffic volume."

Stephen B. Hager, Augustana College, Heidi Trudell, Principia College, Kelly J. McKay, BioEco Research and Monitoring Center, Stephanie M. Crandall, University of Illinois Extension, and Lance Mayer, Iowa City, IA, "Bird density and mortality at windows."

Heath M. Hagy, Richard M. Kaminski, Samuel K. Riffell, and Francisco J. Vilella, Mississippi State University, and Kenneth J. Reinecke, USGS Patuxent Wildlife Research Center, "Winter waterfowl dynamics in managed moist-soil wetlands in the Mississippi Alluvial Valley."

Kelly K. Hallinger, Rebecka L. Brasso, and Daniel A. Cristol, College of William and Mary, "Lifetime fitness of Tree Swallows exposed to aquatic mercury."

Maura F. Hanna, Canisius College, Richard Keith and Brenda Keith, Kalamazoo Nature Center, and Sara R. Morris, Canisius College, "Morphological differences in Gray Catbirds across age classes."

Alan "Bruce" Hitch and J. B. Grand, Auburn University, "Do avian abundances differ between habitat types? Implications for assessment of habitat quality."

Mikaela G. Howie and Dan A. Cristol, College of William and Mary, "The infiltration of aquatic mercury into a terrestrial ecosystem."

Austin L. Hughes, University of South Carolina, "Temporal pattern of vocalization type usage in singing sessions of male tyrant flycatchers."

Douglas A. James and Ragupathy Kannan, University of Arkansas, "Nesting habitat of the Great Hornbill (*Buceros bocornis*) in the Anaimalai Hills of southern India."

L. Scott Johnson, Susan L. Balenger, and Brian S. Masters, Towson University, "Do extra-marital affairs make Mountain Bluebirds blue?"

Daniel Klem Jr., Muhlenberg College, "Preventing bird-glass collisions."

Christine Lattin, Eastern Kentucky University, "Is song length an important signal of aggression for Blue Grosbeaks? A playback experiment."

Timothy J. Ludwick and Alan M. Fedynich, Caesar Kleberg Wildlife Research Institute, Glenn H. Perrigo, Texas A&M University-Kingsville, and T. Wayne Swertner, Texas Parks and Wildlife Department, "Nesting ecology of urban columbids in South Texas."

Alan D. Maccarone, Friends University, John N. Brzorad, Lenoir-Rhyne College, and Heather M. Stone, Friends University, "Characteristics and energetics of Great Egret and Snowy Egret foraging flights."

Andrew J. McGann and Robert L. Curry, Villanova University, "Songs of the critically endangered Cozumel Thrasher: what would a needle in a haystack sound like?"

Bailey D. McKay, University of Minnesota, "Phylogeography of the Yellow-throated Warbler (*Dendroica dominica*)."

Karl E. Miller, Florida Fish and Wildlife Conservation Commission, "Impacts of Hurricane Charley on a Florida Scrub-Jay population."

Timothy J. O'Connell, Oklahoma State University, "Investigating the use of Partners in Flight scores for ecological assessment."

Laura M. Palasz and Philip C. Stouffer, Louisiana State University, "Assessment of Henslow's Sparrow abundance and habitat selection across Louisiana."

Emily Pifer, Purple Martin Conservation Association, John R. Sauer and Jane Fallon, USGS Patuxent Wildlife Research Center, and John Tautin, Purple Martin Conservation Association, "Hurricane Katrina: did it affect Purple Martins and Purple Martin roosts?"

Matthew J. Reetz and Kathryn E. Sieving, University of Florida, and Scott K. Robinson, Florida Museum of Natural History, "Responses of four songbird species to experimental cowbird parasitism in a recently invaded area."

Paul G. Rodewald, Ashley A. Buchanan, and Stephen N. Matthews, The Ohio State University, "Stopover behavior of migrant landbirds in two fragmented landscapes: lakeshore and inland regions of Ohio."

Scott A. Rush, University of Georgia, E. C. Soehren, Alabama Department of Conservation and Natural Resources, A. T. Fisk, University of Windsor, M. S. Woodrey, Mississippi State University, and R. J. Cooper, University of Georgia, "Habitat use by marsh birds along the northern Gulf of Mexico with focus on Clapper Rails."

Jean-Pierre L. Savard, Environment Canada, and Bruno Drolet and Melanie L. Cousineau, Canadian Wildlife Service, "Evidence of a five-year population cycle in Rusty Blackbirds (*Euphagus carolinus*)."

John A. Smallwood, Montclair State University, Mark F. Causey, Damascus, MD. David Mossop, Yukon College. James R. Klucsarits, Alvernia College, Bob and Sue Robertson, Kempton, PA, Richard J. Melvin, American Kestrel Foundation, Joey Mason, Middleboro, MA, Michael J. Maurer, Marion, MA, John W. Parrish Jr., and Timothy F. Breen, Georgia Southern University, Kenneth Boyd, Fort Gordon, GA, Russell D. Dawson, University of Northern British Columbia, and Gary R. Bortolotti, University of Saskatchewan, "Why are American Kestrel (*Falco sparverius*) populations declining in North America? Evidence from nest box programs."

Amanda B. Stockwell and Ryanne Sullivan, Canisius College, Richard Keith and Brenda Keith, Kalamazoo Nature Center, and Sara R. Morris, Canisius College, "Migration and stopover ecology of the Tennessee Warbler at an inland stopover site near Kalamazoo, Michigan."

Antoinette Taylor, Philip C. Stouffer, and Michael J. Chamberlain, Louisiana State University, "Effects of site preparation on breeding birds in early successional Louisiana pine plantations."

Sarah E. Warner, W. Gregory Shriver, and Marnie A. Pepper, University of Delaware, "Tidal marsh breeding birds as bioindicators of mercury contamination along the Delaware Bay."

Jill Wick and Yong Wang, Alabama A&M University, "Home range size and habitat use of two songbird species in forest stands treated with prescribed fire and thinning."

Michael Wierda, Clemson University, and

Jacqueline Bird, Alen Rebertus, and Alec Linsay, Northern Michigan University, "Foraging ecology of Pileated Woodpeckers in Duke's Experimental Forest in the Upper Peninsula of Michigan."

Amanda Jo Williams, Jennifer C. Owen, and Frank R. Moore, University of Southern Mississippi, and Mary Garvin, Oberlin College, "Changes in immunocompetence of the Gray Catbird during an experimental West Nile virus infection."

Stefan Woltmann and Thomas W. Sherry, Tulane University, "Territory fidelity and age structure in a tropical understory bird, Chestnut-backed Antbird (*Myrmeciza exsul*)."

POSTERS

Lyndell M. Bade, University of Missouri-St. Louis, Colleen Crank, Missouri Botanical Garden & Litzsinger Road Ecology Center, Kathleen Beilsmith, Parkway North High School, St. Louis, MO, and Patricia G. Parker, University of Missouri-St. Louis, "Reproductive ecology of the Eurasian Tree Sparrow in two suburban environments in St. Louis."

Eric Beck, Michael Husak, and Michael A. Patten, Cameron University and University of Oklahoma, "Oklahoma marshbird monitoring project."

Bethany Belock and Doris Watt, Saint Mary's College, "An examination of the role of weight, plumage color, cere color and total area of UV reflectant plumage on mate selection in Budgerigars (*Melopsitticus undulates*)."

Mary Bomberger Brown, University of Nebraska, "The Tern and Plover Conservation Partnership: a model for interior Least Tern and Piping Plover conservation."

Ashley A. Buchanan and Paul G. Rodewald, The Ohio State University, "Movements, habitat selection, and stopover duration of migrant songbirds in the western Lake Erie Basin of Ohio."

John P. Carpenter, Yong Wang, and Hugh Metcalfe, Alabama A&M University, "Cerulean Warbler home range estimates and roost site selection in northeast Alabama."

Jason Courter and Gary Ritchison, Eastern Kentucky University, "Responses of flocks of Tufted Titmice to different-sized raptors."

Mark Deutschlander, Hobart and William Smith Colleges, and Rachel Muheim and John Phillips, Virginia Polytechnic Institute, "White-throated Sparrows use polarization cues on the horizon to calibrate their magnetic compass at sunrise and sunset."

Kathryn Dirks, Molly Grove, Angela Roles, and Mary Garvin, Oberlin College, "DNA sequence-based identification of rootlets used in Gray Catbird (*Dumetella carolinensis*) nest linings."

Ryan M. Dziedzic and Michael J. Hamas, Central Michigan University, "Seasonal use of dynamic Lake Huron coastal habitats by migrating shorebirds."

Rodney K. Felix Jr., and Robb Diehl, University of Southern Mississippi, and Janet M. Ruth, U.S. Geological Survey, "Passerine migratory movements aloft in the southwestern United States."

Katherina Forgues, Trent University, Canada, "Making the connection between shorebirds and off-road vehicles."

Ilana Garcia-Grossman, Lydia Moore, Harden Wisebram, Alice Manos, and Mary Garvin, Oberlin College, "Feeding preference of *Culex pipiens* between two potential West Nile virus reservoir host species."

Andrew D. George, Timothy J. O'Connell, Karen R. Hickman, and David M. Leslie Jr., Oklahoma State University, "Avian response to Old World bluestem *Bothriochloa ischaemum* monocultures in mixed grass prairie."

Lewis Grove, Emma DeLeon, Ben Coulter, Michael Lanzone, and Andrew L. Mack, Carnegie Museum of Natural History, "Automatic detection of recorded nocturnal flight calls: a comparison of methods."

Stephen B. Hager, Christopher R. Bertram, and Katie R. Derner, Augustana College, "Breeding birds and nest productivity at Green Wing Environmental Laboratory, northcentral Illinois."

Christy Hand and Patrick Jodice, Clemson University, and Felicia Sanders, Santee Coastal Reserve, "Research on the half shell: diet composition of American Oystercatchers during the non-breeding season."

R. Ian Horn and Gary K. Ritchison, Eastern Kentucky University, "Eastern Phoebes use different strategies to provision young."

Jason D. Jacobs, Canisius College, Kristen M. Covino, University of Maine, and Sara R. Morris, Canisius College, "Seasonal differ-

ences in energetic condition of Blackpoll Warblers on Appledore Island."

Jodie M. Jawor and Jocole Green, University of Southern Mississippi, "Steroid hormones and immune function in Northern Cardinals (*Cardinalis cardinalis*)."

Erik I. Johnson and Philip C. Stouffer, Louisiana State University, "Ectoparasites affect bird condition in neotropical forest fragments."

Kelly Kussmaul and Doris Watt, Saint Mary's College, "Heterophil to lymphocyte ratios as indicators of stress in Budgerigars (*Melopsittacus undulates*) under different housing arrangements."

Kristen M. Lear and Edward H. Burtt Jr., Ohio Wesleyan University, "Bacterial degradation of flight and body contour feathers by *B. licheniformis*."

Katherine Leith, Michael Wierda, and William Bowerman, Clemson University, James Sikarskie, Michigan State University, Dave Best, U.S. Fish and Wildlife Service, and Teryl Grubb, U.S. Forest Service, "Using factor analysis as a tool for the improvement of field sampling strategies."

William B. Lewis, E. Dale Kennedy, and Douglas W. White, Albion College, "Analysis of the vocalizations of the Northern Cardinal (*Cardinalis cardinalis*)."

Timothy Ludwick, Autumn Smith, and Alan Fedynich, Caesar Kleberg Wildlife Research Institute, "A comparative study of feeding habits and helminth diversity in south Texas doves."

Kimberly Martinczak and Doris Watt, Saint Mary's College, "Relationships between dominance measures and physical characteristics of the Budgerigar (*Melopsittacus undulates*)."

Kelly J. McKay, BioEco Research and Monitoring Center, and Stephen B. Hager, Augustana College, "The birds of Green Wing Environmental Laboratory in northcentral Illinois."

Marks McWhorter, Mary Brown, and Jennifer C. Owen, University of Southern Mississippi, "Spleen size and activity as it relates to migratory disposition in the Gray Catbird (*Dumetella carolinensis*)."

Zoltán Németh, Michael J. Sellers, Jennifer C. Owen, and Frank R. Moore, University of Southern Mississippi, "Phenotypic organ flexibility around the annual cycle in two Nearctic-neotropical migratory thrush species."

Meredith Palmer and Edward H. Burtt Jr., Ohio Wesleyan University, "Resistance of turaco feathers to bacterial degradation."

Heidi L. Puckett, L. Wes Burger Jr., and Samuel K. Riffell, Mississippi State University, "Mid-contract management effects on breeding grassland songbirds in CP33 habitat buffers in eastern Mississippi."

Orin Robinson, John Dindo, and Lauren Showalter, Dauphin Island Sea Laboratory, "Post Katrina monitoring of nesting birds in coastal Alabama."

Emily Runnells, Hobart and William Smith Colleges, David Bonter, Cornell Laboratory of Ornithology, and Mark Deutschlander, Hobart and William Smith Colleges, "Fat stores and energetic condition of *Catharus* thrushes during spring and autumn migration at a Great Lakes stopover site."

Chad Soard and Gary Ritchison, Eastern Kentucky University, "Carolina Chickadee calls encode information about predator threat."

S. J. Stefan, F. J. Sanders, B. C. Doyle, M. Hughes, and P. G. R. Jodice, College of Charleston, "Seasonal variations in recoveries of South Carolina-banded Brown Pelicans and Royal Terns: a comparison of two seabird species experiencing a decline in local nesting numbers."

Jack M. Stenger and Edward H. Burtt Jr., Ohio Wesleyan University, "The bacterial degradation of phaeomelanic and eumelanic feathers."

Bethany K. Stephan and Anna Marie Parise, Canisius College, Michael Hamilton and Robert L. DeLeon, Buffalo Ornithological Society, and H. David Sheets and Sara R. Morris, Canisius College, "Comparison of avifauna in three riparian environments in western New York: the impact of anthropogenic habitat alteration."

Ryanne Sullivan and Amanda B. Stockwell, Canisius College, Richard Keith and Brenda Keith, Kalamazoo Nature Center, and Sara R. Morris, Canisius College, "Annual variation in the stopover ecology of the Tennessee Warbler in Michigan."

James W. Tucker Jr., Gregory R. Schrott, and Reed Bowman, Archbold Biological Station, "Habitat selection in the endangered

Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*)."

James W. Tucker Jr., Gregory R. Schrott, and Reed Bowman, Archbold Biological Station, "Occupancy modeling to examine detection probabilities and population trends of the endangered Florida Grasshopper Sparrow."

John M. Waud, Rochester Institute of Technology, Omar Gordillo, Comisión Nacional de Áreas Naturales Protegidas, Tuxtla Gutierrez, Mexico, David Mathiason, Rochester Institute of Technology, and Mark Deutschlander, Hobart and William Smith Colleges, "Avian species as indicators of riparian function in Chiapas, Mexico."

Melinda J. Welton, Gulf Coast Bird Observatory, David L. Anderson, Louisiana State University, Gabriel J. Colorado, Universidad Nacional de Colombia, Colombia, and Tiffany A. Beachy, University of Tennessee, "Migration stopover of the Cerulean Warbler (*Dendroica cerulea*) in northern Middle America."

Rebecca Whelan, Tera Levin, and Mary Garvin, Oberlin College, "Detection of volatiles in the uropygial gland secretions of Gray Catbirds (*Dumetella carolinensis*) through solid-phase microextraction head space sampling and gas-chromatograph-mass spectrometry."

Michael Wierda, William Bowerman, Amy Roe, Kathryn Parmentier, William Bridges, and Katherine Leith, Clemson University, James Sikarskie, Michigan State University, David Best, U.S. Fish and Wildlife Service, Teryl Grubb, U.S. Forest Service, and Dennis Bush, Michigan DEQ, "Michigan Bald Eagle Biosentinel Program, monitoring trends of persistent organic pollutants in Great Lakes ecosystems."

Sean M. Williams and Edward H. Burtt Jr., Ohio Wesleyan University, and Ralph W. Schreiber and Elizabeth A. Schreiber, Smithsonian Institution, "Structure of albino feathers: why so weak?"

Meredith P. Wilson and Edward H. Burtt Jr., Ohio Wesleyan University, "Dynamics of *Staphylococcus aureus* on bird feathers."

ATTENDANCE

ALABAMA: *Auburn*, Alan T. Hitch, Brian W. Rolek; *Montgomery*, Lauren M. Showalter, John A. Trent; *Normal*, John P. Carpenter, Lisa M. Gardner Barillas, Leela Pahl, Jill M. Wick, Yong Wang.

ARKANSAS: *Fayetteville*, Elizabeth M. Adam, Douglas A. James.

ARIZONA: *Flagstaff*, Eben H. Paxton; *Tucson*, Clait E. Braun.

CALIFORNIA: *Arcata*, John E. Hunter; *Berkeley* Jennifer M. Wang.

COLORADO: *Denver*, Dennis B. Williams.

DELAWARE: *Newark*, Jeffrey Buler, Sarah E. Goodwin, Gregory W. Shriver, Sarah Warner.

FLORIDA: *Ft. Myers*, Bette J. S. Jackson, Jerome A. Jackson; *Gainesville*, Karl E. Miller, Matthew Reetz; *Lake Placid*, Reed Bowman, Fred Lohrer, Gregory R. Schrott, James W. Tucker; *Orlando*, Reed F. Noss; *Tallahassee*, Jim Cox.

GEORGIA: *Athens*, Scott A. Rush; *Commerce*, Constance Head.

ILLINOIS: *Rock Island*, Stephen B. Hager.

INDIANA: *Notre Dame*, Beth Belock, Kelly Kussmaul, Kim Martinczak, Doris Watt; *South Bend*, Melinda M. Clark.

KANSAS: *Sterling*, Anthony C. Dalisio; *Wichita*, Alan D. Maccarone, Heather M. Stone.

KENTUCKY: *Richmond*, Jason R. Courter, Richard I. Horn, Christine R. Lattin, Gary Ritchison.

LOUISIANA: *Baton Rouge*, David L. Anderson, Curtis W. Burney, Erik I. Johnson, Laura M. Palasz, Antoinette Taylor; *Lafayette*, Maggie Luent; *New Orleans*, Mollie Cashner, Katherine E. Law, Sedge Woltmann, Stefan Woltmann; *Shreveport*, James L. Ingold.

MARYLAND: *Chevy Chase*, Ellen Paul; *Towson*, Scott L. Johnson.

MICHIGAN: *Albion*, Megan Fitzpatrick, E. Dale Kennedy, Will Lewis, Douglas White; *Ann Arbor*, Robert Payne, Laura Payne; *East Lansing*, Kimberly R. Hall; *Mount Pleasant*, Ryan M. Dziedzic, Michael J. Hamas.

MINNESOTA: *St. Paul*, Bailey McKay.

MISSOURI: *St. Louis*, Lyndell M. Bade.

MISSISSIPPI: *Biloxi*, Ian Woodrey, Lorie Woodrey, Mark Woodrey; *Hattiesburg*, Mary (Francie) Brown, M. Susan Devries, Robb Diehl, Rodney K. Felix Jr., Rodney K. Felix Sr., Sheri Glowinski-Matamoros, Jodie Jawor, Marks McWhorter, Frank R. Moore, Zoltan Nemeth, Jen C. Owen, Michael Sellers, Jaclyn Smolinsky, Sarah Wheeless, Amanda J. Wil-

liams; *Mississippi State,* Heath M. Hagy, Heidi L. Puckett; *Stoneville*, Paul B. Hamel.

Montana: *Polson*, Charles R. Blem.

North Carolina: *Hickory*, John N. Brzorad.

Nebraska: *Lincoln*, Mary Bomberger Brown.

New Jersey: *New Brunswick,* Bertram G. Murray Jr.; *Randolph*, John A. Smallwood.

New York: *Bowmansville*, Bethany Stephan; *Buffalo*, Peggy E. Buckley, Katie A. Chmielowiec, Maura Hanna, Jason Jacobs, Amanda Stockwell, Ryanne Sullivan; *Geneva*, Mark E. Deutschlander, Emily S. Runnells; *Grand Island,* Sara R. Morris, Elizabeth Morris; *Rochester*, John M. Waud.

Ohio: *Columbus*, Sandra L. L. Gaunt, Paul G. Rodewald; *Delaware*, Edward H. Burtt Jr., Kristen M. Lear, Meredith Palmer, Jack M. Stenger, Sean M. Williams, Meredith P. Wilson; *Oberlin*, Kathryn Dirks, Ilana Garcia-Grossman, Mary C. Garvin, Tera Levin, Elizabeth Wisebram; *Sandusky*, Robert C. Beason; *Wilmington*, David N. Bonter, Bonnie Keller, Bob Powell.

Oklahoma: *Lawton*, Eric J. Beck; *Stillwater*, Vincent S. Cavalieri, Andrew D. George, Timothy J. O'Connell, Paul van Els; *Tahlequah*, Mia R. Revels.

Pennsylvania: *Allentown*, Daniel Klem Jr., Peter G. Saenger; *Erie,* Emily Pifer, Margaret A. Voss; *Rector*, Adrienne Jo Leppold, Andrew L. Mack; *Villanova*, Robert L. Curry, Andrew J. McGann.

South Carolina: *Charleston*, Stacy J. Stefan; *Clemson*, Latice Fuentes, Christy Hand, Katherine F. Leith, Lindsay J. Moore, Peggy Shrum, Michael R. Wierda; *Columbia*, Austin L. Hughes.

Texas: *Kingsville*, Arlene J. Arnold, Timothy Ludwick; *Lake Jackson,* John C. Arvin, Cecilia M. Riley.

Virginia: *Cambridge Springs,* Eugene S. Morton; *Charlottesville*, Charles E. Clarkson; *Dillwyn*, Mike Stinson; *Hampden-Sydney*, Michael D. Collins; *Shipman*, Allen Hale; *Williamsburg*, Jacob Armiger, Ryan Burdge, Kelly K. Hallinger, Mikaela G. Howie.

Vermont: *Dorset*, Elizabeth F. Gilbert; *Northfield*, William H. Barnard.

Washington: *Bainbridge Island,* Lee H. Robinson.

Washington D.C.: Richard C. Banks, Carla Dove, Joseph R. Jehl, Storrs L. Olson.

Canada, Ontario: *Kingston*, Robert C. Dobbs; *Toronto*, James D. Rising, Trudy L. Rising; Quebec: *Sainte-Foy*, Jean-Pierre L. Savard.

The Wilson Journal of Ornithology 120(4):941–942, 2008

REVIEWERS FOR VOLUME 120

Reviewers are the lifeblood of a journal as editors depend on them to help identify manuscripts with merit and offer suggestions to improve the data analysis, overall science, and writing. These individuals receive little recognition, but are extremely important in the process of improving the science and quality of what is published. We thank all of those listed below who served as referees for manuscripts processed (accepted and published, withdrawn, or rejected) after 1 July 2007 through completion of the December 2008 issue of Volume 120. Those shown in **boldface** reviewed more than one manuscript. The Wilson Ornithological Society and the editorial staff are indebted to and thank each person who served as a reviewer.—Clait E. Braun, Editor

J. T. Ackerman, D. G. Ainley, A. P. Aleixo, M. W. Allard, F. A. Amidon, V. Amrhein, R. G. Anthony, P. Arcese, **W. Arendt**, A. Arjun, R. A. Askins, A. S. Aspbury, S. Austin-Bythell, F. Bairlein, M. C. Baker, G. A. Baldassarre, B. R. Barber, C. Barber, P. F. Battley, R. C. Beason, G. Beauchamp, M. J. Bechard, B. M. Beehler, C. D. Benesh, C. W. Benkman, R. E. Bennetts, R. O. Bierregaard, D. M. Bird, J. G. Blake, P. Blancher, W. J. Bock, D. N. Bonter, S. Boyd, J. T. Boylan, J. D. Brawn, L. A. Brennan, M. Brigham, **D. M. Brooks**, C. R. Brown, D. E. Brown, M. B. Brown, P. A. Buckley, T. M. Burg, A. Burger, L. W. Burger Jr., D. Burhans, R. Burnett, S. L. Burson, E. H. Burtt, R. W. Butler, P. Byholm, E. G. Campbell, R. A. Canterbury, R. E. Carleton, J. Carpenter, J. H. Carter III, C. Cassaday, J. N. Caudell, D. Cerasale, J. Chaves, D. Cimprich, R. Clapp, C. J. Clark, E. D. Clotfelter, R. R. Cohen, R. A. Cole, N. J. Collar, J. A. Collazo, C. T. Collins, M. W. Collopy, M. A. Colwell, **R. N. Conner**, C. J. Conway, S. J. Cooper, S. M. Correa, M. C. Coulter, D. A. Cristol, J. P. Croxall, S. Dale, N. B. Davies, S. K. Davis, S. R. DeKort, R. S. DeLotelle, J. L. Deppe, K. C. Derrickson, A. A. Dhondt, J. G. Dickson, D. R. Diefenbach, R. Diehl, J. J. Dinsmore, P. F. Doherty Jr., D. D. Dolton, J. J. Dosch, C. J. Dove, V. J. Dreitz, S. Droege, H. Drummond, B. D. Dugger, K. Dugger, E. H. Dunn, P. O. Dunn, J. B. Dunning Jr., E. M. Dzialowski, J. M. Eadie, W. R. Eddleman, **J. C. Eitniear**, R. M. Erwin, P. Escalante, M. Evans, T. D. Evans, J. M. Fair, S. G. Fancy, G. L. Farnsworth, M. J. Fernandez, L. Fishpool, J. A. Fitzsimons, J. Fjeldså, C. H. Flather, T. F. Fondell, J. Foster, M. S. Foster, C. M. Francis, K. E. Franzreb, T. M. Freeberg, B. P. Freymann, S. W. Gabrey, **D. E. Gammon**, J. M. Garcia-C, S. L. L. Gaunt, M. Genovart, R. R. George, S. S. Germaine, J. Gilardi, T. W. Gillespie, M. D. Giovanni, C. B. Goguen, **D. A. Granfors**, T. A. Grant, M. Green, M. C. Green, **H. F. Greeney**, **J. S. Greenlaw**, M. Griesser, **J. A. Grzybowski**, C. G. Guglielmo, R. J. Gutiérrez, M. T. Guzy, J. Haffer, T. M. Haggerty, M. L. Hall, S. Hallager, D. G. Harper, M. Hau, F. E. Hayes, M. A. Hayes, **W. M. Healy**, P. Hendricks, J. Herkert, G. Herring, S. K. Herzog, C. Hill, H. L. Hinam, R. T. Holmes, T. R. Huels, **J. M. Hull**, C. Hunter, R. L. Hutto, L. D. Igl, J. L. Ingold, K. Islam, F. M. Jaksic, D. Jakubas, R. L. Jarvis, **J. R. Jehl Jr.**, W. Jetz, P. H. Johnsgard, D. H. Johnson, L. Johnson, L. S. Johnson, M. D. Johnson, C. D. Jones, H. L. Jones, J. A. Jones, S. L. Jones, J. G. Jorgensen, J. O. Karubian, **E. D. Kennedy**, K. P. Kenow, R. E. Kenward, D. M. Keppie, E. L. Kershner, D. King, D. Klem Jr., S. Kleven, **W. D. Koenig**, O. Komar, D. N. Koons, N. K. Krabbe, A. W. Kratter, M. Krist, J. A. Kushlan, W. P. Kuvlesky, C. Kwit, S. K. Kyle, D. F. Lane, E. K. Latch, S. C. Latta, D. J. Lebbin, M. R. Lein, D. L. Leonard, G. Leonardi, J. Lepson, S. B. Lerman, D. J. Levey, C. A. Lindell, C. D. Littlefield, C. Loiseau, G. A. Londono, **P. E. Lowther**, G. A. Lozano, P. Luttrell, R. S. Lutz, T. J. Mabee, J. R. Madden, **M. L. Mallory**, **R. W. Mannan**, M. Marín, **J. S. Marks**, K. Martin, L. B. Martin, **T. E. Martin**, S. Matsuoka, R. Mauck, I. McAllan, A. E. McAndrews, C. McCaffrey, J. P. McCarty, K. McGraw, M. L. McKinney, M. K. McNicholl, **S. R. McWilliams**, E. Mellink, B. Mila, E. H. Miller, A. P. Møller, D. Monk, F. R. Moore, D. H. Morse, E. S. Morton, H. C. Mueller, D. Mulcahy, R. Nagarajan, N. L. Newfield, V. Nyman, S. H. Oppel, G. H. Orians, J. F. Ornelas, S. Oyler-McCance, **K. C. Parsons**, R. B. Payne, S. F. Pearson, B. S. Pedersen, D. W. Perkins, C. M. Perrins, M. C. Perry, S. E. Peters, B. Pinshow, M. Piorkowski, T. D. Pitts, J. H. Plissner, W. F. Porter, W. Post, R. A. Powell, **H. Pöysä**, V. V. Pravosudov, D. R. C.

Prescott, R. Prinzinger, **R. O. Prum**, **C. Randler**, J. L. Rasmussen, J. T. Ratti, J. C. Reboreda, L. R. Reitsma, K. Renton, M. Restani, M. H. Reynolds, R. T. Reynolds, J. M. Rhymer, N. H. Rice, C. P. Riehl, W. J. Ripple, J. D. Rising, J. W. Rivers, C. S. Robbins, **R. J. Robertson**, J. A. Robinson, S. A. Rohwer, **J. J. Roper**, R. N. Rosenfield, **S. S. Rosenstock**, J. T. Rotenberry, R. R. Roth, A. Roulin, D. Renison, **D. C. Rudolph**, T. B. Ryder, J. Salgado Ortiz, **D. W. Sample**, C. Sanchez, B. K. Sandercock, J. R. Sauer, L. Savoy, R. R. Schaefer, J. A. Schmutz, J. A. Schnack, T. S. Schulenberg, P. L. Schwagmeyer, S. H. Schweitzer, J. M. Scott, S. G. Sealy, N. E. Seavy, **J. A. Sedgwick**, C. L. Seewagen, A. N. Setiawan, J. Shafer, S. Sharbaugh, D. Shutler, **L. M. Siefferman**, C. H. Sieg, L. F. Silveira, M. F. Small, D. W. Smith, R. J. Smith, J. A. Soha, R. Sojda, C. Somers, T. A. Sordahl, D. A. Spector, C. N. Spottiswoode, **M. T. Stanback**, R. D. Stark, D. F. Stauffer, D. W. Steadman, R. B. Stiehl, D. F. Stotz, P. C. Stouffer, B. J. M. Stutchbury, J. N. Styrsky, D. L. Swanson, P. B. Taylor, R. C. Telfair, R. Thorstrom, K. M. C. Tjorve, B. W. Tobalske, E. J. Tramer, J. Traylor, F. Valera, S. Van Balen, A. N. Van Buren, M. F. Vasconelos, C. Vaughan, J. H. Vega Rivera, N. A. M. Verbeek, K. T. Vierling, S. C. Votier, G. E. Wallace, J. R. Walters, Y. Wang, D. J. Watt, K. A. Weakland, P. J. Weatherhead, J. M. Wells, S. West, C. M. White, M. Wikelski, J. W. Wiley, N. Wilkins, M. Williams, S. O. Williams, M. J. Willis, K. S. Winker, H. Winkler, K. Winnett-Murray, **M. Winter**, M. C. Witmer, S. Wolf, M. S. Woodrey, C. Woods, L. G. Woolaver, **J. M. Wunderle Jr.**, R. H. Yahner, T. Yerkes, Y. Yom-Tov, **J. R. Young**, T. Yuri, R. Zambrano, **K. Zyskowski**.

The Wilson Journal of Ornithology 120(4):943–962, 2008

Index to Volume 120, 2008

Compiled by Kathleen G. Beal

This index includes references to genera, species, authors, and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text. Nomenclature follows the AOU Check-list of North American Birds (Seventh Edition) and F. Gill and M. Wright (*Birds of the World, Recommended English names.* Princeton University Press, Princeton, New Jersey and Oxford, United Kingdom). Reference is made to books reviewed and announcements as they appear in the volume.

A

abundance
of *Cypseloides niger* in southern Rocky Mountains Colorado and New Mexico, 331–338
Accentor, Alpine, see *Prunella collaris*
Accipiter gentilis, 239–247
gularis, 96
striatus, 464
Ackerman, Joshua T., John Y. Takekawa, Jill D. Bluso, Julie L. Yee, and Collin A. Eagles-Smith, Gender identification of Caspian Terns using external morphology and discriminant function analysis, 378–383
Acrocephalus arundinaceus, 398
orientalis, 269, 272
Aegolius acadicus, 390
Aegotheles cristatus, 510
Afton, Alan D., see Jonsson, Jon Einar and ———
Agelaius phoeniceus, 342, 470, 820–829
Aguirre, Ray, see Dreibelbis, Justin Z., Kyle B. Melton, ———, Bret A. Collier, Jason Hardin, Nova J. Silvy, and Markus J. Peterson
Aguirre, Ray, see Melton, Kyle B., Justin Z. Dreibelbis, ———, Bret A. Collier, T. Wayne Schwertner, Markus J. Peterson, and Nova J. Silvy
Aimophila aestivalis, 625–627
Akepa, see *Loxops coccineus*
Aleixo, Alexandre, see Tobias, Joseph A., Daniel J. Lebbin, ———, Michael J. Andersen, Edson Guilherme, Peter A. Hosner, and Nathalie Seddon
Alsophis portoricensis, 464
Amakihi, Hawaii, see *Hemignathus virens*
Amazon, Puerto Rican, see *Amazona vittata*
Red-lored, see *Amazona autumnalis*
White-fronted, see *Amazona albifrons*
Yellow-naped, see *Amazona auropalliata*
Amazona
albifrons, 353–365
auropalliata, 353–365
autumnalis, 354, 355
finschi, 176, 357, 361, 363
vittata, 357
Ammer, Frank K., Petra Bohall Wood, and Roger J. McPherson, Gender identification of Grasshopper Sparrows comparing behavioral, morphological, and molecular techniques, 221–225
Ammodramus bairdii, 667–673
henslowii, 111–119
maritimus, 394
savannarum, 111–119, 221–225
Amphispiza bilineata, 569
Anairetes alipinus, 535
parulus, 535, 539, 541
Anas cyanoptera, 390–392
platyrhynchos, 311
wyvilliana, 311–319
Anderson, Michael J., see Tobias, Joseph A., Daniel J. Lebbin, Alexandre Aleixo, ———, Edson Guilherme, Peter A. Hosner, and Nathalie Seddon
Andropadus latirostris, 399
virens, 387, 398–401
Ani, Groove-billed, see *Crotophaga sulcirostris*
Smooth-billed, see *Crotophaga ani*
Anodorhynchus leari, 176
Anous spp., 378
Ant-Tanager, Red-crowned, see *Habia rubica*
Antbird, Chestnut-backed, *see Myrmeciza exsul*
Dusky, see *Cercomacra tyrannina*
Spotted, see *Hylophylax naevioides*
Warbling, see *Hypocnemis cantator*
White-bellied, see *Myrmeciza longipes*
Anthus cervinus, 85
spragueii, 667–673
Antpitta, Rusty-breasted, see *Grallaricula ferrugineipectus*
Antshrike, Western Slaty, see *Thamnophilus atrinucha*
Antunes, Andre Pinassi, see Rohe, Fabio and ———
Aploderma aequatoriale, 249
narina, 249
Aphelocoma ultramarina, 342
Ara macao, 353–365
militaris, 176
rubrogenys, 176
Aratinga canicularis, 353–365
strenua, 357, 361
Arcese, Peter, see Janssen, Michael H., ———, Mark S. Sloan, and Kelly J. Jewell
Arcos-Torres, Agustina, see Solano-Ugalde, Alejandro, and ———
Ardea cinerea, 631–632
herodias, 173
Areta, Juan I., see Niklison, Alina M., ———, Roman A. Ruggera, Karie L. Decker, Carlos Bosque, and Thomas E. Martin
Asio otus, 641–645

Athene cunicularia, 72
Atlapetes semirufus, 856–862
Auklet, Cassin's, see *Ptychoramphus aleuticus*
Automolus infuscatus, 10, 11, 18, 20, 21
leucophthalamus, 10–25, 45
melanopezus, 11
ochrolaemus, 11
paraensis, 10, 11, 20
rufipileatus, 21
rubiginosus, 11
rufipileatus, 11

B

Baeolophus bicolor, 183
Balasubramaniam, Shandiya, and Patrick-Jean Guay, Purple Swamphens (*Porphyrio porphyrio*) attempting to prey upon Black Swan (*Cygnus atratus*) eggs and preying upon a cygnet on an urban lake in Melbourne, Australia, 633–635
Baldwin, Michael J., Wylie C. Barrow Jr., Clinton Jeske, and Frank C. Rohwer, Metabolizable energy in Chinese tallow fruit for Yellow-rumped Warblers, Northern Cardinals, and American Robins, 525–530
Ballard, Grant, see Nur, Nadav, ———, and Geoffrey R. Geupel
Banko, Paul C., see Farmer, Chris, Bridget A. Frederick, ———, Robert M. Stephens, and Carter W. Snow
Barbtail, Spotted, see *Premnoplex brunnescens*
Barrantes, Gilbert, Cesar Sanchez, Branko Hilje, and Rodolfo Jaffe, Male song variation of Green Violetear (*Colibri thalassinus*) in the Talamanca Mountain Range, Costa Rica, 519–524
Barreto, Guillermo R., see Bertsch, Carolina and ———
Barrow Jr., Wylie C., see Baldwin, Michael J., ———, Clinton Jeske, and Frank C. Rohwer
Bartramia longicauda, 129
beaver, American, see *Castor canadensis*
Beckmann, Christa, An intraspecific killing in adult Pacific Reef Egrets (*Egretta sacra*), 422–424
behavior
age influence on territory size, habitat selection, reproductive success in male *Wilsonia canadensis*, 446–454
breeding, adoption then reproduction with father by female *Sialia sialis*, 419–422
courtship behavior of *Andropadus virens*, 398–401
display of male *Phaethornis ruber*, 201–204
ecology of tropical birds, 26–37
feeding
double-scratching by *Xanthocephalus xanthocephalus*, 657–659
factors influencing fidelity of *Carpodacus mexicanus*, 371–377
male *Hemignathus virens* fed *Loxioides bailleui* fledgling, 416–418
of *Tyrannus dominicensis*, 655–657
fledging of *Pyroderus scutatus*, 413–416
flocking of *Spizella wortheni*, 569–574
foraging comparison of juvenile and adult *Turdus migratorius*, 209–213
habitat use by *Mergus serrator*, 743–754
nest defense by *Thryothorus ludovicianus*, 467–472
nocturnal of *Momotus momota*, 653–654
of *Chen caerulescens* and *Chen rossii*, 725–731
of *Cnipodectes superrufus*, 38–49
of *Dryolimnas* [*cuvieri*] *aldabranus*, 50–61
of *Oreomystis bairdi*, 195–199
of *Phalaenoptilus nuttallii*, 505–512
of *Scytalopus simonsi*, 473–477
polyandry in *Melospiza melodia*, 345
polygyny in *Otus flammeolus*, 645–648
post-fledging movement of *Catharus ustulatus*, 62–73
raising of *Molothrus ater* by *Aimophila aestivalis*, 625–627
range extension of *Melospiza georgiana nigrescens*, 393–395
reproductive success of *Dendroica cerulea* in Indiana, 105–110
roosting during winter of *Seiurus aurocapilla* in core foraging area, 455–450
simultaneous incubation by two females and nestling provisioning by four adults at a *Passerculus sandwichensis* nest, 628–630
Bellbird,
Three-wattled, see *Procnias tricarunculatus*
Benham, Phred M., see Reitsma, Leonard R., Michael T. Hallworth, and ———
Benitez-Diaz, Hesiquio, see Honey-Escandon, Magali, Blanca E. Hernandez-Banos, Adolfo G. Navarro-Siguenza, ———, and A. Townsend Peterson
Berry, Lainie and Estanislao Taisacan, Nest success and nest predation of the endangered Rota White-eye (*Zosterops rotensis*), 618–619
Bertsch, Carolina and Guillermo R. Barreta, Diet of the Yellow-knobbed Curassow in the central Venezuelan Llanos, 767–777
Bezy, M. Bernadette, see Matuzak, Greg D., ———, and Donald J. Brightsmith
Biamonte, Esteban, see Sandoval, Luis, Esteban Biamonte, and Alejandro Solana-Ugalde
Biancucci, Luis and Thomas E. Martin, First description of the breeding biology and natural history of the Ochre-breasted Brush Finch (*Atlapetes semirufus*) in Venezuela, 856–862
Bingham, Ralph L., see Breeden, Jeffrey B., Fidel Hernandez, ———, Nova J. Silvy, and Gary L. Waggerman
Bildstein, Keith L., review, 430–431
Birgus latro, 59
Bittern, American, see *Botaurus lentiginosus*
Least, see *Ixobrychus exilis*
Blackbird, Common, see *Turdus merula*
Red-winged, see *Agelaius phoeniceus*
Yellow-headed, see *Xanthocephalus xanthocephalus*
Blackcap, Eurasian, see *Sylvia atricapilla*
Bluebird, Eastern, see *Sialia sialis*
Bluethroat, see *Luscinia svecica*

Bluso, Jill D., see Ackerman, Joshua T., John Y. Takekawa, ———, Julie L. Yee, and Collin A. Eagles-Smith
Bobolink, see *Dolichonyx oryzivorus*
Bombycilla cedrorum, 149, 151, 342
Bonasa umbellus, 239–247 (Frontispiece), 897–900
Bond, Jeanine and Daniel Esler, Bill entanglement in subcutaneously-anchored radio transmitters on Harlequin Ducks, 599–602
Bondo, Kristin J., Lauren N. Gilson, and Reed Bowman, Anvil use by the Red-cockaded Woodpecker, 217–221
Booby, Blue-footed, see *Sula nebouxii*
Bosque, Carlos, see Niklison, Alina M., Juan I. Areta, Roman A. Ruggera, Karie L. Decker, ———, and Thomas E. Martin
Botaurus lentiginosus, 513–518
Bowman, Reed, see Bondo, Kristin J., Lauren N. Gilson, and ———
Brant, Black, see *Branta bernicla nigricans*
Branta bernicla nigricans, 755–766
Breeden, Jeffrey B., Fidel Hernandez, Ralph L. Bingham, Nova J. Silvy, and Gary L. Waggerman, Effects of traffic noise on auditory surveys of urban White-winged Doves, 384–389
breeding biology
  adoption then reproduction with father by female *Sialia sialis,* 419–422
  differences in growth of *Branta bernicila nigricans* between a major breeding colony and outlying breeding aggregations, 755–766
  Grallaricula ferrugineipectus, 345–352
  habitat and other features of *Ficedula narcissina,* 92–98
  long-term trends in breeding in old-growth Adirondack forest and surrounding regions, 153–158
  nests, eggs, and incubation of *Pyrrhula erythaca,* 874–878
  of *Atlapetes semirufus* in Venezuela, 856–862
  of *Pyroderus scutatus granadensis,* 862–867
  parental care in *Sporophila hypoxantha* and *Sporophila collaris,* 879–883
  reproductive success of *Troglodytes aedon* in suburban and rural landscapes, 99–104
  reproductive success of *Vireo latimeri* in a montane habitat, 460–466
  use of legs and feet for control by scoters during aerial courtship, 594–599
Brennan, Leonard A., Texas quails: ecology and management, reviewed, 236–237
Brigham, R. Mark, see Woods, Christopher P. and ———
Brightsmith, Donald J., see Matuzak, Greg D., M. Bernadette Bezy, and ———
Brotogeris jugularis, 353–365
Brown, Charles R., see O'Brien, Valerie A., Amy T. Moore, Kathryn P. Huyvaert, and ———
Brown, David R. and Thomas W. Sherry, Solitary winter roosting of Ovenbirds in core foraging area, 455–459
Bubo virginianus, 173, 239–247, 505, 507
Bucephala clangula, 320–330, 732–742
  islandica, 320–330
Buehler, David A., see Giocomo, James L., E. Daniel Moss, ———, and William G. Minser
Bullfinch, Grey-headed, see *Pyrrhula erythaca,* 874–878
bullfrog, see *Rana catsbeiana*
Bunting, Godlewski's, see *Emberiza godlewskii*
  Indigo, see *Passerina cyanea*
  Lark, see *Calamospiza melanocorys*
  Meadow, see *Emberiza cioides*
  Painted, see *Passerina ciris*
Buren, A. N. Van and P. Dee Boersma, Humboldt Penguins (*Spheniscus humboldti*) in the northern hemisphere,
Burger Jr., L. Wesley, see Wood, Douglas R., Francisco J. Vilella, and ———
Bustos, Oscar Francisco Reyna, see Rosas-Espinoza, Veronica Carolina, Elisa Maya-Elizarraras, ———, and Francisco Martin Huerta-Martinez
Butcher, Jerrod A. see Campomizzi, Andrew J., Shannon L. Ferrell, and ———, Nest site selection by a male Black-capped Vireo
Buteo albicaudatus, 229
  jamaicensis, 229, 422, 708–716
  regalis, 708–716
  swainsoni, 708–716
Byrd, G. Vernon, see Gibson, Daniel D. and ———

C

Cacomantis sepulcralis, 887–890
Cahill, J. R. A., E. Matthysen, and N. E. Huanca, Nesting biology of the Giant Conebill (*Oreomanes fraseri*) in the High Andes of Bolivia, 545–549
Calamospiza melanocorys, 62
Calcarius ornatus, 667–673
  pictus, 398
Calypte anna, 522, 523
Calyptophilus frugivorus, 190
  terius, 190–195
Campomizzi, Andrew J., Shannon L. Ferrell, and Jerrod A. Butcher, Nest site selection by a male Black-capped Vireo, 407–409
Campephilus principalis, 500
Canales-Delgadillo, Julio C., Laura M. Scott-Morales, Mauricio Cotera Correa, and Marisela Pando Moreno, Observations of flocking behavior of Worthen's Sparrows (*Spizella wortheni*) and occurrence in mixed-species flocks, 569–574
Caprimulgus carolinensis, 509
  climacurus, 510
  tristigma, 510
  vociferus, 509, 778–783
Cardiff, Scott G. and Steven M. Goodman, Natural history of the Red Owl (*Tyto soumagnei*) in dry deciduous tropical forest in Madagascar, 891–897
Cardinal, Northern, see *Cardinalis cardinalis*
Cardinalis cardinalis, 99, 103, 149, 150
Carduelis crassirostris, 534
  tristis, 149, 150, 151

Carleton, Renee E., Ectoparasites affect hemoglobin and percentages of immature erythrocytes but not hematocrit in nestling Eastern Bluebirds, 565–568
Carpodacus mexicanus, 342, 371–377
Carrasco, Luis, see Karubian, Jordan and ———
Castor canadensis, 320
cat
  domestic, see *Felis catus [domesticus]*
  feral, see *Felis catus [domesticus]*
Catbird, Gray, see *Dumetella carolinensis*
Catharus bicknelli, 458
  fuscescens, 277–285, 528
  guttatus, 458
  ustulatus, 62–73, 74–84, 157, 277–285, 296–303, 467, 468
Cauchard, Laure, see Overington, Sarah E., ———, and Kinberly-Ann Cote
Centropus toulou, 59
Cercomacra tyrannina, 31, 33
Certhia americana, 155
Cervus elaphus, 830
Cettia annae, 268, 273
  borealis, 268
  carolinae, 273
  cetti, 268
  diphone, 268–276
  fortipes, 268–276
  haddeni, 268–278
  ruficapilla, 268, 273
  seebohmi, 268–276
Chaetura pelagica, 154
Chandler, C. Ray, see Wetzel, Daniel P. and ———
Charadrius melodus, 404–407
  montanus, 700–707
Chat-tanager, Eastern, see *Calyptophilus frugivorus*
  Western, see *Calyptophilus terius*
Chaunus ictericus, 228–230
Chavez-Ramirex, Felipe, see Kim, Daniel H., Wesley E. Newton, Gary R. Lingle, and ———
Chen caerulescens, 422, 725–731
  rossii, 725–731
Chenxi, Jia and Sun Yuehua, Nests, eggs, and incubation behavior of Grey-headed Bullfinch (*Pyrrhula erythaca*), 874–878
Chickadee, Black-capped, see *Poecile atricapillus*
  Boreal, see *Poecile hudsonica*
  Gray-headed, see *Poecile cincta*
chicken, see *Gallus gallus*
Childers, Theresa M. and Stephen J. Dinsmore, Density and abundance of Mountain Plovers in northeastern Montana, 700–707
Chlidonias niger, 167–175, 381
  spp., 376
Chondestes grammacus, 342
Christie, David, see del Hoyo, Jesop, Andrew Elliott, and ———
Chuck-will's-widow, see *Caprimulgus carolinensis*
Cinclodes, Bar-winged, see *Cinclodes fuscus*
Cinclodes fuscus, 475
Circus cyaneus, 173
Cnipodectes subbrunneus, 38–49
  superrufus, 38–49
Coccothraustes vespertinus, 342
Coccyzus americanus, 287
  vieilloti, 464
Cohen, Jonathan B., Elizabeth H. Wunker, and James D. Fraser, Substrate and vegetation selection by nesting Piping Plovers, 404–407
Colaptes auratus, 495
Colibri coruscans, 522, 523
  delphinae, 523
  serrirostris, 523
  thalassinus, 519–524
Collier, Bret A., see Dreibelbis, Justin Z., Kyle B. Melton, Ray Aguirre, ———, Jason Hardin, Nova J. Silvy, and Markus J. Peterson
Collier, Bret A., see Melton, Kyle B., Justin Z. Dreibelbis, Ray Aguirre, ———, T. Wayne Schwertner, Markus J. Peterson, and Nova J. Silvy
Collister, Douglas M., see Wilson, Scott, Keith A. Hobson, ———, and Amy G. Wilson
Compospiza garleppi, 476
Conebill, Chestnut-vented, see *Conirostrum speciosum*
  Cinereous, see *Conirostrum cinereum*
  Giant, see *Oreomanes fraseri*
  Tamurugo, see *Conirostrum tamarugense*
  White-browed, see *Conirostrum ferrugineiventre*
Conirostrum cinereum, 531–544
  ferrugineiventre, 531–544
  speciosum, 548
  tamarugense, 548
Contopus sordidulus, 342
  virens, 146–152, 155, 291, 292
Contreras, Thomas A., see Reetz, Matthew J., Elizabeth Farley, and ———
Conway, Courtney J., see Nadeau, Christopher P., ———, Bradley S. Smith, and Thomas E. Lewis
Coot, American, see *Fulica americana*
Coracias spatulatus, 479
Correa, Mauricio Cotera, see Canales-Delgadillo, Julio C., Laura M. Scott-Morales, ———, and Marisela Pando Moreno
Corvus albus, 59
  brachyrhynchos, 109, 149, 151
  caurinus, 422
  corax, 72, 173
Cotinga cayana, 871–874
Cotinga, Spangled, see *Cotinga cayana*
Cote, Kimberly-Ann, see Overington, Sarah E., Jaure Cauchard, and ———
Coturnicops noveboracensis, 513, 606–610
Coucal, Malagasy, see *Centropus toulou*
Cowbird, Bronzed, see *Molothrus aeneus*
  Brown-headed, see *Molothrus ater*
  Shiny, see *Molothrus bonariensis*
crab, robber, see *Birgus latro*
Craik, Shawn R. and Rodger D. Titman, Movements and habitat use by Red-breasted Merganser broods in eastern New Brunswick, 743–754

Crandall, Stephanie M., see Hager, Stephen B., Heidi Trudell, Kelly J. McKay, ———, and Lance Mayer
Crane, Red-crowned, see *Grus japanensis*
Cranioleuca albicapilla, 535, 538, 541
Crax daubentoni
Creeper, Brown, see *Certhia americana*
Kauai, see *Oreomystis bairdi*
Crotophaga ani, 422
sulcirostris, 214–216
Crow, American, see *Corvus brachyrhynchos*
Northwestern, see *Corvus caurinus*
Pied, see *Corvus albus*
Crypturellus obsoletus, 228–230
Cuckoo, Banded Ground, see *Neomorphus radiolosus*
Puerto Rican Lizard, see *Coccyzus vieilloti*
Rusty-breasted, see *Cacomantis sepulcralis*
Yellow-billed, see *Coccyzus americanus*
Curassow, Yellow-knobbed, see *Crax daubentoni*
Cyanocitta cristata, 109, 114, 149, 467–472
Cygnus atratus, 633–635
Cypseloides niger, 331–338

D

Dacnis, Tit-like, see *Xenodacnis parina*
Davis, Andrew K., Factors influencing fidelity of House Finches to a feeding station, 371–377
Davis Jr., William E., reviews, 231–232, 232–233
Debinski, Diane M., see Olechnowski, Brian F. M. and ———
Decker, Karie L., see Niklison, Alina M., Juan I. Areta, Roman A. Ruggera, ———, Carlos Bosque, and Thomas E. Martin
del Hoyo, Jesop, Andrew Elliott, and David Christie, Handbook of the birds of the world. Volume 11: old world fly-catchers to old world warblers, reviewed, 235–236
Dendrocopus leucotos, 219
[*Picoides*] *major,* 96, 215, 217, 219
medius, 219
minor, 219
syriacus, 219
Dendroica caerulescens, 157, 296–303, 446, 450, 451
cerulea, 105–110
coronata, 155, 290, 296–303, 525–530
discolor, 455, 458
dominica, 401–403
magnolia, 157, 277–285, 296–303
petechia, 289, 291, 292, 451, 470, 830–839
pensylvanica, 155
pinus, 217
tigrina, 455, 458
virens, 157, 409–412
de Queiroz, Alan, Double-scratching by Yellow-headed Blackbirds, 657–659
Desrochers, Andre, see Hadley, Adam and ———
Dessecker, Daniel R., see Zimmerman, Guthrie S., Rick R. Horton, ———, and R. J. Gutierrez
Dickcissel, see *Spiza americana*
Dicrurus hottentottus, 97
macrocercus, 97
Diem, Kenneth L., see Pugesek, Bruce H. and ———
diet
anvil use by *Picoides borealis,* 217–221
foraging ecology of High Andean insectivorous birds in remnant *Polylepis* forest patches, 531–544
freeze-frame fruit selection by birds, 901–905
metabolizable energy in Chinese tallow fruit for *Cardinalis cardinalis, Turdus migratorius, Dendroica coronata,* 525–530
of *Asio otus* in northern and central Negev Desert, Israel, 641–645
of *Crax daubentoni,* 767–777
of *Melanerpes formicivorus* at forest in Mexico, 494–498
of nesting *Charadrius melodus,* 404–407
of nestling Black-crowned Night-herons, 637–640
of *Patagona gigas* ingesting calcium-rich minerals, 651–653
of parrots in a modified landscape, 353–356
of six neotropical bird species, 214–216
use of clay licks by Maroon-fronted Parrots, 176–180
Di Giocomo, Alejandro G., see Facchinetti, Carolina, ———, and Juan C. Reboreda
Dinsmore, Stephen J., see Childers, Theresa M. and ———
Dionne, Mark, Celine Maurice, Jean Gauthier, and Francois Shaffer, Impact of hurricane Wilma on migrating birds: the case of the Chimney Swift, 784–792
Dipsochelys dussumieri, 59
disease
avian cell-mediated immune response to drought, 813–819
no evidence for spring re-introduction of an arbovirus by *Petrochelidon pyrrhonota,* 910–913
trichomoniasis in Band-tailed Pigeons, 603–606
distribution
effects of landscape configuration for *Caprimulgus vociferous,* 778–783
of *Cnipodectes superrufus,* 38–49
of *Cypseloides niger* in southern Rocky Mountains Colorado and New Mexico, 331–338
of *Patagona gigas* in Argentina, 648–651
Diuca speculifera, 613–617
Doerr, Joseph G., see Levad, Richard G., Kim M. Potter, Christopher W. Shultz, Carolyn Gunn, and ———
Dolichonyx oryzivorus, 820–829
D'Orazio, Kelly A. and Diane L. H. Neudorf, Nest defense by Carolina Wrens, 467–472
Dove, Carla and Court Goodroe, Marbled Godwit collides with aircraft at 3,700 m, 914–915
Dove, Mourning, see *Zenaida macroura*
Dreibelbis, Justin Z., see Melton, Kyle B., ———, Ray Aguirre, Bret A. Collier, T. Wayne Schwertner, Markus J. Peterson, and Nova J. Silvy
Dreibelbis, Justin Z., Kyle B. Melton, Ray Aguirre,

Bret A. Collier, Jason Hardin, Nova J. Silvy, and Markus J. Peterson, Predation of Rio Grande Wild Turkey nests on the Edwards Plateau, Texas, 906–910
Droege, Sam, see McNulty, Stacy A., ———, and Raymond D. Masters
Drolet, Bruno, see Robert, Michel, ———, and Jean-Pierre L. Savard
Drongo, Black, see *Dicrurus macrocercus*
Hair-crested, see *Dicrurus hottentottus*
Dryocopus pileatus, 148, 149, 499–504
Dryolimnas [*cuvieri*] *aldabranus*, 50–61
cuvieri, 50, 631–632
Duck, Harlequin, see *Histrionicus histrionicus*
Dugger, Bruce D., see Uyehara, Kimberly J., Andrew Engilis Jr., and ———
Dumetella carolinensis, 146–152, 146–152, 277–285, 287, 291, 292, 297
Dunnock, see *Prunella modularis*

E

Eagle, Bald, see *Haliaeetus leucocephalus*
Eagles-Smith, Collin A., see Ackerman, Joshua T., John Y. Takekawa, Jill D. Bluso, Julie L. Yee, and ———
Eason, Perri K., see Vanderhoff, E. Natasha and ———
ecology
behavior of tropical birds, 26–37
cavity number and use by other species as correlates of group size in *Picoides borealis*, 181–189
Sitta spp., 692–699
winter for *Coturnicops noveboracensis*, 606–610
eggs
abnormal eggs of Rio Grande Wild Turkey, *Meleagris gallopavo*, 226–228
clutch variations of egg size in *Rhea americana*, 674–682
description for *Calyptophilus tertius* and *Xanoligea montana*, 190–195
of *Scytalopus simonsi*, 473–477
Egret, Pacific Reef, see *Egretta sacra*
Egretta sacra, 422–424
Elaenia, Lesser, see *Elaenia chiriquensis*
Yellow-bellied, see *Elaenia flavogaster*
Elaenia chiriquensis, 31, 32
flavogaster, 31, 32
Elaphe alleghaniensis, 420
anomala, 96
obsoleta, 109
spp., 182
Elliot, Andrew, see del Hoyo, Jesop, ———, and David Christie
Ellison, Kevin S., Nest reuse by Vermilion Flycatchers in Texas, 339–344
Emberiza cioides, 97
godlewskii, 97
Empidonax alnorum, 256, 259, 278
flavescens, 278
fulvifrons, 256–267
minimus, 278, 342
occidentalis, 332
oberholseri, 259
traillii, 259, 278, 342, 830–839
traillii extimus, 256
virescens, 256, 278, 342
Engilis Jr., Andrew, see Uyehara, Kimberly J., ———, and Bruce D. Dugger
Epicrates inornatus, 464
Erithacus rubecula, 209
Esler, Daniel, see Bond, Jeanine and ———, Bill entanglement in subcutaneously-anchored radio transmitters on Harlequin Ducks, 599–602
Estades, Cristian, M. Angelica Vukasovic, and Jorge A. Tomasevic, Giant Hummingbirds (*Patagona gigas*) ingest calcium-rich minerals, 651–653
Eudyptes spp., 575–581
Eugenes fulgens, 522
Euphonia gouldi, 200–201
Euphonia, Olive-backed, see *Euphonia gouldi*
Euptilotis neoxenus, 249
Evers, Erin M., see Linkhart, Brian D., ———, Julie D. Megler, Eric C. Palm, Catherine M. Salipante, and Scott W. Yanco

F

Faaborg, John, see White, Jennifer D. and ———
Facchinetti, Carolina, Alejandro G. Di Giacomo, and Juan C. Reboreda, Parental care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) seedeaters, 879–883
Fair, J. M. and S. J. Whitaker, Avian cell-mediated immune response to drought, 813–819
Fairy-Wren, Red-backed, see *Malurus melanocephalus*
Falco newtoni, 59
Farley, Elizabeth, see Reetz, Matthew J., ———, and Thomas A. Contreras
Farmer, Chris, Bridget A. Frederick, Paul C. Banko, Robert M. Stephens, and Carter W. Snow, Palila (*Loxioides bailleui*) fledgling fed by Hawaii Amakihi (*Hemignathus virens*), 416–418
Felis catus, [*domesticus*], 60, 190, 194
Felton, Adam, Annika M. Felton, and David B. Lindenmayer, The display of a Reddish Hermit (*Phaethornis ruber*) in a lowland rainforest, Bolivia, 201–204
Felton, Annika M., see Felton, Adam, ———, and David B. Lindenmayer
Fernandez, Eladio M., see Rimmer, Christopher C., Lance G. Woolaver, Rina K. Nichols, ———, Steven C. Latta, and Esteban Garrido
Fernandez, Gustavo J. and Juan C. Reboreda, Between and within clutch variation of egg size in Greater Rheas, 674–682
Ferrell, Shannon L., see Campomizzi, Andrew J., ———, and Jerrod A. Butcher, Nest site selection by a male Black-capped Vireo
Ficedula albicollis, 96, 97
hypoleuca, 96, 97, 446
parva, 96, 97
zanthopygia, 92–98

Finch, Cochabamba Mountain, see *Compospiza garleppi*
House, see *Carpodacus mexicanus*
Ochre-breasted Brush, see *Atlapetes semirufus*
White-winged Diuca, see *Diuca speculifera*
Flamingo, Greater, see *Phoenicopterus roseus*
Flicker, Northern, see *Colaptes auratus*
Flycatcher, Acadian, see *Empidonax virescens*
Alder, See *Empidonax alnorum*
Ash-throated, see *Myiarchus cinerascens*
Collared, see *Ficedula albicollis*
Cordilleran, see *Empidonax occidentalis*
Dusky, see *Empidonax oberholseri*
European Pied, see *Ficedula hypoleuca*
Great Crested, see *Myiarchus crinitus*
Narcissus, see *Ficedula narcissina*
Red-breasted, see *Ficedula parva*
Southwestern Willow, see *Empidonax traillii extimus*
Vermilion, see *Pyrocephalus rubinus*
Willow, see *Empidonax traillii*
Yellow-rumped, see *Ficedula zanthopygia*
Foliage-gleaner, Buff-throated, see *Automolus ochrolaemus*
Chestnut-crowned, see *Automolus rufipileatus*
Olive-backed, see *Automolus infuscautus*
Para, see *Automolus paraensis*
Ruddy, see *Automolus rubiginosus*
White-eyed, see *Automolus leucophthalamus*
Forest-Falcon, Barred, see *Micrastur ruficollis*
Collared, see *Micrastur semitorquatus*
Foster, Mercedes S., Freeze-frame fruit selection by birds, 901–905
fox, red, see *Vulpes vulpes*
Francisco, Mercival R., Paulo R. R. Oliveira Jr., and Vitor O. Lunardi, Nest and fledglings of the Red-ruffed Fruitcrow (*Pyroderus scutatus*), 413–416
Fraser, James D., see Cohen, Jonathan B., Elizabeth H. Wunker, and ———
Fraser, M. J., see Robertson, C. J. R., P. Hyvonen, ———, and C. R. Pickard
Frederick, Bridget A., see Farmer, Chris, ———, Paul C. Banko, Robert M. Stephens, and Carter W. Snow
Freymann, Bernd P. and Karl-Ludwig Schuchmann, Postnatal growth rates of hummingbirds: review and new records, 884–887
Fruitcrow, Red-ruffed, see *Pyroderus scutatus*
Fry, W. Roger, see Oehler, David A., Steve Pelikan, ———, Leonard Weakley Jr., Alejandro Kusch, and Manuel Marin
Fulica americana, 513–518
Fulmar, Northern, see *Fulmarus glacialis*
Fulmarus glacialis, 635–636

G

Gallinula chloropus, 513–518
Gallinule, Purple, see *Porphyrio martinicus*
Gallus gallus, 399, 474, 479
Garrido, Esteban, see Rimmer, Christopher C., Lance G. Woolaver, Rina K. Nichols, Eladio M. Fernandez, Steven C. Latta, and ———
Garrido, Esteban, see Townsend, Jason M., ———, and Danilo A. Mejia
Garrulus glandarius, 72, 96
Gauthier, Gilles, see Senechal, Helene, ———, and Jean-Pierre L. Savard
gecko, house, see *Hemidactylus frenatus*
Genetics
of breeding and wintering population of *Limnothlypis swainsonii*, 433–445
of martin species, 683–691
Geococcyx spp., 206
George, T. Luke, see Sperry, Jinelle H., ———, and Steve Zack
Geospiza scandens, 31
Geothlypis trichas, 80, 146–152, 277–285, 286–295, 288, 291, 292, 296–303, 830–839
Geupel, Geoffrey R., see Nur, Nadav, Grant Ballard, and ———
Gibson, Daniel D. and G. Vernon Byrd, Birds of the Aleutian Islands, Alaska, reviewed, 425–426
Gilson, Lauren N., see Bondo, Kristin J., ———, and Reed Bowman
Giocomo, James L., E. Daniel Moss, David A. Buehler, and William G. Minser, Nesting biology of grassland birds at Fort Campbell, Kentucky and Tennessee, 111–119
Glaucidium bolivianum, 548
Glaucomys volans, 181–189
Gnatcatcher, Black-tailed, see *Polioptila melanura*
Blue-gray, see *Polioptila caerulea*
Godwit, Marbled, see *Limosa fedoa*
Goldeneye, Barrow's, see *Bucephala islandica*
Common, see *Bucephala clangula*
Goldfinch, American, see *Carduelis tristis*
Goodman, Steven M., see Cardiff, Scott G. and ———
Goodroe, Court, see Dove, Carla and ———
Goose, Lesser Snow, see *Chen caerulescens*
Ross's, see *Chen rossi*
Goshawk, Northern, see *Accipiter gentilis*
Grackle, Boat-tailed, see *Quiscalus major*
Common, see *Quiscalus quiscula*
Great-tailed, see *Quiscalus mexicanus*
Grallaricula ferrugineipectus, 345–352
flavirostris, 348, 349
nana, 348, 349
peruviana, 348, 349
Grassquit, Blue-black, see *Volatinia jacarina*
Graves, Gary R., review, 233–235
Graves, Gary R., see Winker, Kevin and ———
Grebe, Pied-billed, see *Podilymbus podiceps*
Greenbul, Little, see *Andropadus virens*
Yellow-whiskered, see *Andropadus latirostris*
Grim, Tomas, Begging behavior of fledgling Rusty-breasted Cuckoo (*Cacomantis sepulcralis*), 887–890
Grosbeak, Evening, see *Coccothraustes vespertinus*
Rose-breasted, see *Pheucticus ludovicianus*
Grouse, Ruffed, see *Bonasa umbellus*

Grus japonensis, 610–613
Guay, Patrick-Jean, see Balasubramaniam, Shandiya and ———
Guilherme, Edson, see Tobias, Joseph A., Daniel J. Lebbin, Alexandre Aleixo, Michael J. Andersen, ———, Peter A. Hosner, and Nathalie Seddon
Gull, Black-backed, see *Larus marinus*
California, see *Larus californicus*
Franklin's, see *Larus pipixcan*
Western, see *Larus occidentalis*
Gunn, Carolyn, see Levad, Richard G., Kim M. Potter, Christopher W. Shultz, ———, and Joseph G. Doerr
Gustafson, Mary, review, 235–236
Gutierrez, R. J., see Zimmerman, Guthrie S., Rick R. Horton, Daniel R. Dessecker, and ———
Gymnorhinus cyanocephalus, 217

H

Habia rubica, 12
habitat
age influence on selection by male *Wilsonia canadensis,* 446–454
bird responses to managed forested landscape, 897–900
comparison of effect of burned and unburned habitats on *Junco hymenalis,* 131
features of breeding *Bucephala islandica* in eastern Canada, 320–330
influence of grazing and available moisture on breeding densities of grassland birds in central Platte River Valley, Nebraska, 820–829
long-term effects of wastewater irrigation on habitat and a bird community in central Pennsylvania, 146–152
of nesting *Charadrius melodus,* 404–407
of *Tyto soumagnei* in Madagascar, 891–897
preference of *Neomorphus radiolosus,* 205–209
quality of anthropogenic habitats for *Vermivora chrysoptera* in central Pennsylvania, 801–812
riparian bird species response to vegetation and local habitat features, 840–855
riparian willow habitat of songbirds in Greater Yellowstone Ecosystem, 830–839
selection by *Dendroica cerulea* in Indiana, 105–110
selection by *Picoides borealis,* 793–800
use by fledged *Catharus ustulatus,* 62–73
wetland features that influence occupancy by *Anas wyvilliana,* 311–319
winter use by *Poecile hudsonica,* 139–145
Hadley, Adam and Andre Desrochers, Winter habitat use by Boreal Chickadee flocks in a managed forest, 139–145
Hager, Stephen B., Heidi Trudell, Kelly J. McKay, Stephanie M. Crandall, and Lance Mayer, Bird density and mortality at windows, 550–564
Haley, Katherin L., see Mojica, Elizabeth K., J. Michael Meyers, Brian A. Millsap, and ———
Haliaeetus leucocephalus, 304–330
Hall, C. Scott and Stephen W. Kress, Diet of nestling Black-crowned Night-herons in a mixed species colony: implications for tern conservation, 637–640
Hallworth, Michael T., see Reitsma, Leonard R., ———, and Phred M. Benham
Hamao, Shoji, Maria J. S. Veluz, Takema Saitoh, and Isao Nishiumi, Phylogenetic relationship and song differences between closely related Bush Warblers, (*Cettia seebohmi* and *C. diphone*), 268–276
Hanson, Thor, First observation of duetting in the Olive-backed Euphonia (*Euphonia gouldi*), 200–201
Hardin, Jason, see Dreibelbis, Justin Z., Kyle B. Melton, Ray Aguirre, Bret A. Collier, ———, Nova J. Silvy, and Markus J. Peterson
Hardy, Douglas R. and Spencer P. Hardy, White-winged Diuca Finch (*Diuca speculifera*) nesting on Quelccaya Ice Cap, Peru, 613–617
hare, snowshoe, see *Lepus americanus*
Harrier, Northern, see *Circus cyaneus*
Hawk, Red-tailed, see *Buteo jamaicensis*
Sharp-shinned, see *Accipiter striatus*
White-tailed, see *Buteo albicaudatus*
Hawk-Owl, Togian, see *Ninox burhani*
Heath, Shane R. and Frederick A. Servello, Effects of predation and food provisioning on Black Tern chick survival, 167–175
Helmitheros vermivorum [*vermivorus*], 280
Hemidactylus frenatus, 215
Hemignathus virens, 416–418
Hermit, Reddish, see *Phaethornis ruber*
Hernandez, Fidel, see Breeden, Jeffrey B., ———, Ralph L. Bingham, Nova J. Silvy, and Gary L. Waggerman
Hernandez-Banos, Blanca E., see Honey-Escandon, Magali, ———, Adolfo G. Navarro-Siguenza, Hesiquio Benitez-Diaz and A. Townsend Peterson
Heron, Great Blue, see *Ardea herodias*
Grey, see *Ardea cinerea*
Highland-tanager, Hispaniolan, see *Xenoligea montana*
Hilje, Branko, see Barrantes, Gilbert, Cesar Sanchez, ———, and Rodolfo Jaffe
Hill, Geoffrey E., Ivorybill hunters: the search for proof in a flooded wilderness, reviewed, 232–233
Hirundo rustica, 214
Histrionicus histrionicus, 599–602
Hobson, Keith A., see Wilson, Scott, ———, Douglas M. Collister, and Amy G. Wilson
Hockey, Philip A. R., see Wanless, Ross M. and ———
Hoeflich, Ernesto C. Enkerlin, see Valdes-Pena, Rene A., Sonia Gabriela Ortiz-Maciel, Simon O. Valdez Juarez, ———, and Noel F. R. Snyder
home range
for post-fledging grassland birds, 120–130
Honey-Escandon, Magali, Blanca E. Hernandez-Banos, Adolfo G. Navarro-Siguenza, Hesiquio Benitez-Diaz, and A. Townsend Peterson, Phy-

logeographic patterns of differentiation in the Acorn Woodpecker, 478–493
Horton, Rick R., see Zimmerman, Guthrie S., ———, Daniel R. Dessecker, and R. J. Gutierrez
Hosner, Peter A. and Noemi E. Huanca, Nest, eggs, and parental care of the Puna Tapaculo (*Scytalopus simonsi*), 473–477
Hosner, Peter A., see Tobias, Joseph A., Daniel J. Lebbin, Alexandre Aleixo, Michael J. Andersen, Edson Guilherme, ———, and Nathalie Seddon
Huanca, N. E., see Cahill, J. R. A., E. Matthysen, and ———
Huanca, Noemi E., see Hosner, Peter A. and ———
Hubbard, Michael W., see Wells, Kimberly M. Suedkamp, Joshua J. Millspaugh, Mark R. Ryan, and ———
Huerta-Martinez, Francisco Martin, see Rosas-Espinoza, Veronica Carolina, Elisa Maya-Elizarraras, Oscar Francisco Reyna Bustos, and ———
Hummingbird, Amethyst-throated, see *Lampornis amethystinus*
Anna's, see *Calypte anna*
Blue-throated, see *Lampornis clemenciae*
Giant, see *Patagona gigas*
Magnificent, see *Eugenes fulgens*
Huyvaert, Kathryn P., see O'Brien, Valerie A., Amy T. Moore, ———, and Charles R. Brown
Hylocichla mustelina, 62, 64, 70, 127, 146–152, 155, 277–285, 296–303, 342
Hylophylax naevioides, 27, 29
Hypocnemis cantator, 33
Hyvonen, P., see Robertson, C. J. R., ———, M. J. Fraser, and C. R. Pickard

I

Icterus cucullatus, 342
dominicensis, 462
galbula, 297
parisorum, 342
Ictinia mississippiensis, 287
Indrawan, Mochamad, Pamela C. Rasmussen, and Sunarto, A new White-Eye (*Zosterops*) from the Togian Islands, Sulawesi, Indonesia, 1–9
Ingels, Johan, Nest, nestling care, and breeding season of the Spangled Cotinga (*Cotinga cayana*) in French Guiana, 871–874
Islam, Kamal, see Roth, Kirk L. and ———
Islam, Zafar-Ul, see Menon, Shaily, ———, Jorge Soberon, and A. Townsend Peterson
Ixobrychus exilis, 513–518

J

Jackson, Jerome A., George Miksch Sutton: artist, scientist, and teacher, reviewed, 231–232
jaeger, see *Stercorarius* spp.
Jaeger, Long-tailed, see *Stercorarius longicaudus*
Jaffe, Rodolfo, see Barrantes, Gilbert, Cesar Sanchez, Branko Hilje, and ———
Janssen, Michael H., Peter Arcese, Mark S. Sloan, and Kelly J. Jewell, Polyandry and sex ratio in the Song Sparrow, 395–398
Jay, Blue, see *Cyanocitta cristata*
Eurasian, see *Garrulus glandarius*
Mexican, see *Aphelocoma ultramarina*
Pinyon, see *Gymnorhinus cyanocephalus*
Jeske, Clinton, see Baldwin, Michael J., Wylie C. Barrow Jr., ———, and Frank C. Rohwer
Jewell, Kelly J., see Janssen, Michael H., Peter Arcese, Mark S. Sloan, and ———
Johnson, Andrew B. and Kevin Winker, Autumn stopover near the Gulf of Honduras by Nearctic-Neotropic migrants, 277–285
Johnson, L. Scott, see Newhouse, Michael J., Peter P. Marra, and ———
Jonsson, Jon Einar and Alan D. Afton, Lesser Snow Geese and Ross's Geese form mixed flocks during winter but differ in family maintenance and social status, 725–731
Juarez, Simon O. Valdez, see Valdes-Pena, Rene A., Sonia Gabriela Ortiz-Maciel, ———, Ernesto C. Enkerlin Hoeflich, and Noel F. R. Snyder
Junco, Dark-eyed, see *Junco hyemalis*
Junco hyemalis, 131–138, 283, 342
Junglefowl, Red, see *Gallus gallus*

K

Kappes Jr., John J., Cavity number and use by other species as correlates of group size in Red-cockaded Woodpeckers, 181–189
Karubian, Jordan and Luis Carrasco, Home range and habitat preferences of the Banded Ground-cuckoo (*Neomorphus radiolosus*), 205–209
Kestrel, Madagascar see *Falco newtoni*
Kim, Daniel H., Wesley E. Newton, Gary R. Lingle, and Felipe Chavez-Ramirez, Influence of grazing and available moisture on breeding densities of grassland birds in the central Platte River Valley, Nebraska, 820–829
Kingbird, Eastern, see *Tyrannus tyrannus*
Grey, see *Tyrannus dominicensis*
Kinglet, Golden-crowned, see *Regulus satrapa*
Kirschel, Alexander N. G., Novel courtship behavior in the Little Greenbul (*Andropadus virens*), 398–401
Kite, Mississippi, see *Ictinia mississippiensis*
kittiwake, see *Rissa* spp.
Kittiwake, Black-legged, see *Rissa tridactyla*
Klippenstine, Dwight R. and Spencer G. Sealy, Differential ejection of cowbird eggs and non-mimetic eggs by grassland passerines, 667–673
Koenig, Walter D., see Stromberg, Mark R., ———, Eric L. Walters, and John Schweisinger
Kress, Stephen W. see Hall, C. Scott and ———
Kubel, Jacob E. and Richard H. Yahner, Quality of anthropogenic habitats for Golden-winged Warblers in central Pennsylvania, 801–812
Kusch, Alejandro, see Oehler, David A., Steve Pelikan, W. Roger Fry, Leonard Weakley Jr., ———, and Manuel Marin

L

Lampornis amethystinus, 522
  clemenciae, 522
  viridipallens, 522
Lanius ludovicianus, 342
Larus californicus, 159–166
  marinus, 505
  occidentalis, 505
  pipixcan, 422
Laterallus jamaicensis, 513, 514
Latta, Steven C., see Rimmer, Christopher C., Lance G. Woolaver, Rina K. Nichols, Eladio M. Fernandez, ———, and Esteban Garrido
Leader, Zohar, Yoram Yom-Tov, and Uzi Motro, Diet of the Long-eared Owl in the northern and central Negev Desert, Israel, 641–645
Lebbin, Daniel J., see Tobias, Joseph A., ———, Alexandre Aleixo, Michael J. Andersen, Edson Guilherme, Peter A. Hosner, and Nathalie Seddon
Lehman, Paul, review, 425–426
Lein, M. Ross, Song variation in Buff-breasted Flycatchers (*Empidonax fulvifrons*), 256–267
Leptasthenura adicola, 537
  xenothorax, 534, 537
  yanacensis, 531–544
Lepus americanus, 245
Leslie Jr., David M., see McConnell, Scott, Timothy J. O'Connell, and ———
Levad, Richard G., Kim M. Potter, Christopher W. Shultz, Carolyn Gunn, and Joseph G. Doerr, Distribution, abundance, and nest-site characteristics of Black Swifts in the southern Rocky Mountains of Colorado and New Mexico, 331–338
Lewis, Thomas E., see Nadeau, Christopher P., Courtney J. Conway, Bradley S. Smith, and ———
Li, Feng, see Wang, Qiang and ———
Licata, Diane, see Muir, James A., ———, and Thomas E. Martin
Limnothlypis swainsonii, 433–445
Limosa fedoa, 914–915
Lindberg, Mark S., see Safine, David E. and ———
Lindenmayer, David B., see Felton, Adam, Annika M. Felton, and ———
Lingle, Gary R., see Kim, Daniel H., Wesley E. Newton, ———, and Felipe Chaves-Ramires
Linkhart, Brian D., Erin M. Evers, Julie D. Megler, Eric C. Palm, Catherine M. Salipante, and Scott W. Yanco, First observed instance of polygyny in Flammulated Owls, 645–648
Lloyd, Huw, Foraging ecology of High Andean insectivorous birds in remnant *Polylepis* forest patches, 531–544
Longspur, Chestnut-collared, see *Calcarius ornatus*
  Smith's, see *Calcarius pictus*
Lophodytes cucullatus, 732–742
Lorenz, Stephan and Sampath Seneveratne, Northern Fulmar predation of Common Murre, 635–636
Loxioides bailleui, 31, 416–418
Loxops coccineus, 28
Lundari, Vitor O., see Francisco, Mercival R., Paulo R. R. Oliveira Jr., and ———
Luscinia megarhynchos, 254, 387

M

Macaw, Lears, see *Anodorhynchus leari*
  Military, see *Ara militaris*
  Red-fronted, see *Ara rubrogenys*
  Scarlet, see *Ara macao*
Macrodipteryx longipennis, 510
Magpie, Red-billed Blue, see *Urocissa erythrorhyncha*
Mallard, see *Anas platyrhynchos*
Malurus melanocephalus, 398
Manacus vitellinus, 32
Manakin, Golden-collared, see *Manacus vitellinus*
Margarops fuscatus, 464
Marin, Manuel, see Oehler, David A., Steve Pelikan, W. Roger Fry, Leonard Weakley Jr., Alejandro Kusch, and ———
Marra, Peter P., see Newhouse, Michael J., ———, and L. Scott Johnson
martin, see *Progne* spp.
Martin, Sand, see *Riparia riparia*
Martin, Thomas E., see Biancucci, Luis and ———
Martin, Thomas E., see Muir, James A., Diane Licata, and ———
Martin, Thomas E., see Niklison, Alina M., Juan I. Areta, Roman A. Ruggera, Karie L. Decker, Carlos Bosque, and ———
Masters, Raymond D., see McNulty, Stacy A., Sam Droege, and ———
Matthysen, E., see Cahill, J. R. A., ———, and N. E. Huanca
Matuzak, Greg D., M. Bernadette Bezy, and Donald J. Brightsmith, Foraging ecology of parrots in a modified landscape: seasonal trends and introduced species, 353–365
Maurice, Celine, see Dionne, Mark, ———, Jean Gauthier, and Francois Shaffer
Maya-Elizarraras, Elisa, see Rosas-Espinoza, Veronica Carolina, ———, Oscar Francisco Reyna Bustos, and Francisco Martin Huerta-Martinez
Mayer, Lance, see Hager, Stephen B., Heidi Trudell, Kelly J. McKay, Stephanie M. Crandall, and ———
McCaffery, Brian J., see Renner, Heather M. and ———
McCarthy, Eugene M., Handbook of avian hybrids of the world, reviewed, 233–235
McConnell, Scott, Timothy J. O'Connell, and David M. Leslie Jr., Land cover associations of nesting territories of three sympatric buteos in shortgrass prairie, 708–716
McCracken, Kevin G., see Wilson, Robert E. and ———
McKay, Bailey D., A recording of a type B song of the Yellow-throated Warbler, 401–403
McKay, Kelly J., see Hager, Stephen B., Heidi Trudell, ———, Stephanie M. Crandall, and Lance Mayer

McKinnon, Emily Anne and Raleigh J. Robertson, The signal function of a melanin-based plumage ornament in Golden-winged Warblers, 366–370.
McNulty, Stacy A., Sam Droege, and Raymond D. Masters, Long-term trends in breeding birds in an old-growth Adirondack forest and the surrounding region, 153–158
McPherson, Roger J., see Ammer, Frank K., Petra Bohall Wood, and ———
Meadowlark, Eastern, see *Sturnella magna*
Meadowlark, Western, see *Sturnella neglecta*
Megadyptes antipodes, 378
Megler, Julie D., see Linkhart, Brian D., Erin M. Evers, ———, Eric C. Palm, Catherine M. Salipante, and Scott W. Yanco
Meijia, Danilo A., see Townsend, Jason M., Esteban Garrido, and ———
Melanerpes albeolus, 486
angustifrons, 486
aurifrons, 479, 495
carolinus, 149, 181–189, 219, 220
erythrocephalus, 219
flavifrons, 219
flavigula, 486
formicivorus, 219, 478–493, 494–498
hoffmanni, 214–216
hypopolius, 219
lewis, 219, 479
lineatus, 486
pucherani, 479
pygmaeus, 479
striatipectus, 486
uropygialis, 479, 495
Melanitta fusca, 582–593
spp., 594–599
Meleagris gallopavo, 226–228, 906–910
ocellata, 229
Melospiza georgiana, 257
georgiana nigrescens, 393–395
melodia, 146–152, 297, 342, 395–398, 470
Melozone leucotis, 214
sp., 214
Melton, Kyle B., Justin Z. Dreibelbis, Ray Aguirre, Bret A. Collier, T. Wayne Schwertner, Markus J. Peterson, and Nova J. Silvy, Abnormal eggs of Rio Grande Wild Turkeys on the Edwards Plateau, Texas, 226–228.
Melton, Kyle B., see Dreibelbis, Justin Z., ———, Ray Aguirre, Bret A. Collier, Jason Hardin, Nova J. Silvy, and Markus J. Peterson
Mennill, Daniel J., see Tremain, Sarah B., Kyle A. Swiston, and ———
Menon, Shaily, Zafar-Ul, Islam, Jorge Soberon, and A. Townsend Peterson, Preliminary analysis of the ecology and geography of the Asian nuthatches (Aves: Sittidae), 692–699
Merganser, Hooded, see *Lophodytes cucullatus*
Red-breasted, see *Mergus serrator*
Mergus serrator, 743–754
methods
effect of traffic noise on auditory surveys of urban *Zenaida asiatica,* 384–389
gender identification of *Ammodramus savannarum* comparing behavioral, morphological, and molecular techniques, 221–225
gender identification of *Sterna caspia* using external morphology, 378–383
maximizing detection probability of wetland-dependent birds during point-count surveys in northwestern Florida, 513–518
Meyers, J. Michale, see Mojica, Elizabeth K., ———, Brian A. Millsap, and Katherin L. Haley
Micrastur ruficollis, 228–230
semitorquatus, 229
Microligea palustris, 194
migration
autumn stopover of Nearctic and Neotropic migrants near the Gulf of Honduras, 277–285
changes of migratory landbirds during stopovers in a New York City park, 296–303
effect of hurricane Wilma on migrating *Chaetura pelagica,* 784–792
of Florida subadult *Haliaeetus leucocephalus,* 304–310
stopover of migrating birds in New Orleans, Louisiana in relation to weather, 286–295
stopover of migrating *Catharus ustulatus* in southwest Costa Rica, 74–84
Millsap, Brian A., see Mojica, Elizabeth K., J. Michael Meyers, ———, and Katherin L. Haley
Millspaugh, Joshua J., see Wells, Kimberly M. Suedkamp, ———, Mark R. Ryan, and Michael W. Hubbard
Minus polyglottos, 528, 717–724
mink, see *Mustela vison*
Minser, William G., see Giocomo, James L., E. Daniel Moss, David A. Buehler, and ———
Mockingbird, Northern, see *Minus polyglottos*
Mojica, Elizabeth K., J. Michael Meyers, Brian A. Millsap, and Katherin L. Haley, Migration of Florida subadult Bald Eagles, 304–310
Molothrus aeneus, 287
ater, 113, 114, 149, 340, 467–472, 625–627, 667–673, 820–829
bonariensis, 460–466
Momotus momota, 214–216, 653–654
Monticola gularis, 97
solitarius, 97
Moore, Amy T., see O'Brien, Valerie A., ———, Kathryn P. Huyvaert, and Charles R. Brown
Moorhen, Common, see *Gallinula chloropus*
Moreno, Marisela Pando, see Canales-Delgadillo, Julio C., Laura M. Scott-Morales, Mauricio Cotera Correa, and ———
morphology
gender identification of *Sterna caspia* using external morphology, 378–383
specimen shrinkage in Cinnamon Teal, 390–392
mortality or injury
at windows, 550–564

Limosa fedoa collides with aircraft at 3,700 m, 914–915
of Band-tailed Pigeons, 603–606
of fledgling, subadult, and adult *Larus californicus,* 159–166
Porphyrio porphyrio attempting to prey upon *Cygnus atratus,* 633–635
predation by *Ardea cinerea* on *Dryolimnas cuvieri aldabranus,* 631–632
predation of *Uria aalge* by *Fulmarus glacialis,* 635–636
Morton, Eugene S., see Stutchbury, Bridget J. M. and ———
Moss, E. Daniel, see Giocomo, James L., ———, David A. Buehler, and William G. Minser
Motacilla alba, 85
flava, 89
tschutschensis, 85–91
Motmot, Blue-crowned, see *Momotus momota*
Motro, Uzi, see Leader, Zohar, Yoram Yom-Tov, and ———
Mountain-gem, Green-throated, see *Lampornis viridipallens*
Moyle, Robert G., Beth Slikas, Linda A. Whittingham, David W. Winkler, and Frederick H. Sheldon, DNA sequence assessment of phylogenetic relationships among New World martins (Hirundinidae: *Progne*), 683–691
Muir, James A., Diane Licata, and Thomas E. Martin, Reproductive biology the Red-ruffed Fruitcrow (*Pyroderus scutatus granadensis*), 862–867
Murre, Common, see *Uria aalge*
Mustela gularis, 96
spp., 88
vison, 173
Myadestes townsendi, 332, 342
Myiarchus cinerascens, 813–819
crinitus, 148, 149, 183, 287
Myrmeciza exsul, 33
longipes, 29, 30, 33
Myrmotherul snowi, 20
unicolor, 20

N

Nadeau, Christopher P., Courtney J. Conway, Bradley S. Smith, and Thomas E. Lewis, Maximizing detection probability of wetland-dependent birds during point-count surveys in northwestern Florida, 513–518
natural history
Dryolimnas [*cuvieri*] *aldabranus,* 50–61
Grallaricula ferrugineipectus, 345–352
Navarro-Siguenza, Adolfo G., see Honey-Escandon, Magali, Blanca E. Hernandez-Banos, ———, Hesiquio Benitez-Diaz, and A. Townsend Peterson
Neomorphus radiolosus, 205–209
nest
and nesting behavior of *Tachycineta euchrysea,* 867–871
and nestling care of *Cotinga cayana,* 871–874
defense by *Thryothorus ludovicianus,* 467–472
description for *Calyptophilus tertius* and *Xenoligea montana,* 190–195
habitat selection by *Melanitta fusca,* 582–593
of *Pyroderus scutatus,* 413–416
of *Scytalopus simonsi,* 473–477
raising by *Grus japonensis,* 610–613
reuse by *Pyrocephalus rubinus* in Texas, 339–344
site characteristics of *Cypseloides niger* in southern Rocky Mountains Colorado and New Mexico, 331–338
success and predation of *Zosterops rotensis,* 618–619
nesting
ecology of *Bucephala clangula* and *Lophodytes cucullatus,* 732–742
of *Buteo* spp., 708–716
of grassland birds at Fort Campbell, Kentucky and Tennessee, 111–119
of *Oreomanes fraseri,* 545–549
of *Oreomystis bairdi,* 195–199
nestling
postnatal growth rates of hummingbirds, 884–887
survival of *Chlidonias niger,* 167–175
Neudorf, Diane L. H., see D'Orazio, Kelly A. and ———
Newhouse, Michael J., Peter P. Marra, and L. Scott Johnson, Reproductive success of House Wrens in suburban and rural landscapes, 99–104
Newton, Wesley E., see Kim, Daniel H., ———, Gary R. Lingle, and Felipe Chavez-Ramirez
Nichols, Rina K., see Rimmer, Christopher C., Lance G. Woolaver, ———, Eladio M. Fernandez, Steven C. Latta, and Esteban Garrido
Nicolai, Christopher A., James S. Sedinger, and Michael L. Wege, Differences in growth of Black Brant goslings between a major breeding colony and outlying breeding aggregations, 755–766
Night-heron, Black-crowned, see *Nycticorax nycticorax*
Nightingale, Common, see *Luscinia megarhynchos*
Nightjar, Freckled, see *Caprimulgus tristigma*
Long-tailed, see *Caprimulgus climacurus*
Standard-winged, see *Macrodipteryx longipennis*
Niklison, Alina M., Juan I. Areta, Roman A. Ruggera, Karie L. Decker, Carlos Bosque, and Thomas E. Martin, Natural history and breeding biology of the Rusty-breasted Antpitta (*Grallaricula ferrugineipectus*), 345–352
Ninox burhani, 8
Nishiumi, Isao, see Hamao, Shoji, Maria J. S. Veluz, Takema Saitoh, and ———
noddy, see *Anous* spp.
Nucifraga columbiana, 217
Nur, Nadav, Grant Ballard, and Geoffrey R. Geupel, Regional analysis of riparian bird species response to vegetation and local habitat features, 840–855
Nutcracker, Clark's, see *Nucifraga columbiana*
Nuthatch, Brown-headed, see *Sitta pusilla*

Pygmy, see *Sitta pygmaea*
Red-breasted, see *Sitta canadensis*
White-breasted, see *Sitta carolinensis*
Nycticorax nycticorax, 173, 637–640

O

O'Brien, Valerie A., Amy T. Moore, Kathryn P. Huyvaert, and Charles R. Brown, No evidence for spring re-introduction of an arbovirus by Cliff Swallows, 910–913
O'Connell, Timothy J., see McConnell, Scott, ———, and David M. Leslie Jr.
Odontophorus hyperythrus, 207
Oehler, David A., Steve Pelikan, W. Roger Fry, Leonard Weakley Jr., Alejandro Kusch, and Manuel Marin, Status of Crested Penguin (*Eudyptes* spp.) populations on three islands in southern Chile, 575–581
Oenanthe oenanthe, 80, 342
Olechnowski, Brian F. M. and Diane M. Debinski, Response of songbirds to riparian willow habitat structure in the Greater Yellowstone Ecosystem, 830–839
Oliveira Jr., Paulo R. R., see Francisco, Mercival R., ———, and Vitor O. Lunardi
Oporornis formosus, 277–285
tolmiei, 478
Oreomanes fraseri, 531–544, 545–549
Oreomystis bairdi, 195–199
Oriole, Baltimore, see *Icterus galbula*
Greater Antillean, see *Icterus dominicensis*
Hooded, see *Icterus cucullatus*
Scott's, see *Icterus parisorum*
Ortiz-Maciel, Sonia Gabriela, see Valdes-Pena, Rene A., ———, Simon O. Valdez Juarez, Ernesto C. Enkerlin Hoeflich, and Noel F. R. Snyder
Otus flammeolus, 645–648
Ovenbird, see *Seiurus aurocapilla* [*auricapillus*]
Overington, Sarah E., Laure Cauchard, and Kimberly-Ann Cote, Kleptoparasitism by Grey Kingbirds (*Tyrannus dominicensis*) in Barbados, 655–657
Owl, Black-and-white, see *Strix nigrolineata*
Burrowing, see *Athene cunicularia*
Great Gray, see *Strix nebulosa*
Great Horned, see *Bubo virginianus*
Long-eared, see *Asio* otus
Madagascar Red, see *Tyto soumagnei*
Northern Saw-whet, see *Aegolius acadicus*
Owlet-Nightjar, see *Aegotheles cristatus*

P

Palila, see *Loxioides bailleui*
Palm, Eric C., see Linkhart, Brian D., Erin M. Evers, Julie D. Megler, ———, Catherine M. Salipante, and Scott W. Yanco
Parakeet, Orange-chinned, see *Brotogeris jugularis*
Orange-fronted, see *Aratinga canicularis*
Pacific, see *Aratinga strenua*
Reddish-bellied, see *Pyrrhura frontalis*
Parrot, Grey, see *Psittacus erithacus*
Lilac-crowned, see *Amazona finschi*
Maroon-fronted, see *Rhynchopsitta terrisi*
Scaly-headed, see *Pionus maximiliani*
Thick-billed, see *Rhynchopsitta pachyrhyncha*
Parula, Northern, see *Parula americana*
Parula americana, 155, 157, 455, 458
Parus major, 387, 446
Passer domesticus, 30, 121, 368, 391, 422
Passerculus sandwichensis, 394, 628–630, 667–673
Passerella iliaca, 830–839
Passerina ciris, 342
cyanea, 146–152, 277–285, 286–295
Patagioenas fasciata, 603–606
Patagioenas plumbea, 228–230
Patagona gigas, 648–651, 651–653
Paxton, Barton J., see Watts, Bryan D., Michael D. Wilson, Fletcher M. Smith, ———, and J. Bill Williams
Pelikan, Steve, see Oehler, David A., ———, W. Roger Fry, Leonard Weakley Jr., Alejandro Kusch, and Manuel Marin
Penguin, Yellow-eyed, see *Megadyptes antipodes*
Perlut, Noah G., see Zalik, Nathan J. and ———
Peterson, A. Townsend, see Honey-Escandon, Magali, Blanca E. Hernandez-Banos, Adolfo G. Navarro-Siguenza, Hesiquio Benitez-Diaz, and ———
Peterson, A. Townsend, see Menon, Shaily, Zafar-Ul, Islam, Jorge Soberon, and ———
Peterson, Markus J., see Dreibelbis, Justin Z., Kyle B. Melton, Ray Aguirre, Bret A. Collier, Jason Hardin, Nova J. Silvy, and ———
Peterson, Markus J., see Melton, Kyle B., Justin Z. Dreibelbis, Ray Aguirre, Bret A. Collier, T. Wayne Schwertner, ———, and Nova J. Silvy
Petrochelidon pyrrhonota, 910–913
Phaethornis ruber, 201–204
Phalacrocorax spp., 376
Phalaenoptilus nuttallii, 505–512
Pheucticus ludovicianus, 149, 151
Philydor atricapillus, 20
novaesi, 20
Phoenicopterus roseus, 121
Phylloscartes ceciliae, 20
Phylloscopus borealis, 85
trochilus, 388
Pickard, C. R., see Robertson, C. J. R., P. Hyvonen, M. J. Fraser, and ———
Picoides albolarvatus, 217, 219
arizonae, 495
borealis, 181–189, 217–221, 793–800
pubescens, 150, 219
scalaris, 495
villosus, 148, 149, 155, 217, 219
Picus viridis, 219
Pigeon, Band-tailed, see *Patagioenas fasciata*
Plumbeous, see *Patagioenas plumbea*
Pionus maximiliani, 357
Pipilo crissalis, 342
erythrophthalmus, 149, 150, 151
maculatus, 342

Pipit, Red-throated, see *Anthus cervinus*
Sprague's, see *Anthus spragueii*
Pistorius, Pierre A., Grey Heron (*Ardea cinerea*) predation on the Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus*), 631–632
Plover, Mountain, see *Charadrius montanus*
Piping, see *Charadrius melodus*
plumage
of *Vermivora chrysoptera,* 366–370
Podilymbus podiceps, 514
Poecile atricapillus, 139–145, 150, 155, 367
cincta, 139, 143
hudsonica, 139–145
montana, 97
palustris, 97
Polioptila caerulea, 287
melanura, 342
Pooecetes gramineus, 667–673
Poorwill, Common, see *Phalaenoptilus nuttallii*
population
cycles in *Bonasa umbellus,* 239–247
of *Charadrius montanus* in northeastern Montana, 700–707
of *Eudyptes* spp. in southern Chile, 575–581
sex ratio in *Melospiza melodia,* 395–398
Porphyrio martinicus, 513–518
Porphyrio porphyrio, 633–635
Porzana carolina, 514
Post, William, Winter ecology of Yellow Rails based on South Carolina specimens, 606–610
Potter, Kim M., see Levad, Richard G., ———, Christopher W. Shultz, Carolyn Gunn, and Joseph G. Doerr
Powell, Shawn C., see Yaukey, Peter H. and ———
Prairie-Chicken, Greater, see *Tympanuchus cupido*
Predation
at nests of *Meleagris gallapavo,* 906–910
at nests of *Thamnophilus atrinucha,* 620–624
by *Micrastur ruficollis* on relatively large prey, 228–230
effects on *Chlidonias niger,* 167–175
intraspecific killing by *Egretta sacra,* 422–424
Premnoplex brunnescens, 476
Price, J. Jordan, see Reichard, Dustin G. and ———
Priotelus roseigaster, 249
proceedings
eighty-ninth annual meeting, 927–940
Procnias tricarunculatus, 522
Procyon lotor, 114, 173
Progne spp., 683–691
subis, 287
Protonotaria citrea, 455, 458
Prunella collaris, 397, 398
modularis, 397
Psittacus erithacus, 176
Ptychoramphus aleuticus, 505
Puffinus puffinus, 505
spp., 378
Pugesek, Bruce H. and Kenneth L. Diem, Timing and location of mortality of fledgling, subadult, and adult California Gulls, 159–166
Pygmy-Owl, Yungas, see *Glaucidium bolivianum*
Pyrocephalus rubinus, 339–344
Pyroderus scutatus, 413–416, 862–867
Pyrrhula erythaca, 874–878
Pyrrhura frontalis, 357

Q

Quail, Mountain Wood, see *Odontophorus hyperythrus*
Quetzal, Eared, see *Euptilotis neoxenus*
Quiscalus major, 342
mexicanus, 342
quiscula, 149

R

raccoon, see *Procyon lotor*
Rail, Aldabra, see *Dryolimnas* [*cuvieri*] *aldabranus*
Black, see *Laterallus jamaicensis*
Clapper, see *Rallus longirostris*
King, see *Rallus elegans*
Virginia, see *Rallus limicola*
White-throated, see *Dryolimnas cuvieri*
Yellow, see *Coturnicops noveboracensis*
Rallus elegans, 514, 515
limicola, 513
longirostris, 513–518
Rana catsbeiana, 312
range
annual and seasonal use by *Picoides borealis,* 793–800
of breeding *Melospiza georgiana migrescens,* 393–395
of *Neomorphus radiolosus,* 205–209
phylogeographic patterns of *Melanerpes formicivorus,* 478–493
Rasmussen, Pamela C., see Indrawan, Mochamad, ———, and Sunarto
rat, see *Rattus* spp.
black, see *Rattus rattus*
Norway, see *Rattus norvegicus*
Rattus norvegicus, 60, 194
rattus, 59, 194
spp., 190, 458
Raven, Common, see *Corvus corax*
Reboreda, Juan C., see Facchinetti, Carolina, Alejandro G. Di Giacomo, and ———
Reboreda, Juan C., see Fernandez, Gustavo J., and ———
Redstart, American, see *Setophaga ruticilla*
Reetz, Matthew J., Elizabeth Farley, and Thomas A. Contreras, Evidence for Bachman's Sparrow raising Brown-headed Cowbirds to fledging, 625–627
Regulus satrapa, 155
Reichard, Dustin G. and J. Jordan Price, Species recognition in a vocal mimic: repetition pattern not the only cue used by Northern Mockingbirds in discriminating songs of conspecifics and Brown Thrashers, 717–724
Reitsma, Leonard R., Michael T. Hallworth, and Phred M. Benham, Does age influence territory size,

habitat selection, and reproductive success of male Canada Warblers in central New Hampshire? 446–454
Renner, Heather M. and Brian J. McCaffery, Demography of Eastern Yellow Wagtails at Cape Romanzof, Alaska, 85–91
report
editor comments, 237
reproduction
does age influence reproductive success of male *Wilsonia canadensis,* 446–454
Rhea, Greater, see *Rhea americana*
Rhea americana, 674–682
Rhynchopsitta pachyrhyncha, 176
terrisi, 176–180
Riehl, Christina, Communal calling and prospecting by Black-headed Trogons (*Trogon melanocephalus*), 248–255
Rimmer, Christopher C., Lance G. Woolaver, Rina K. Nichols, Eladio M. Fernandez, Steven C. Latta, and Esteban Garrido, First description of nests and eggs of two Hispaniolan endemic species: Western Chat-tanager (*Calyptophilus tertius*) and Hispaniolan Highland-tanager (*Xenoligea montana*), 190–195
Riparia riparia, 399
Rissa spp., 378
tridactyla, 399
Robert, Michel, Bruno Drolet, and Jean-Pierre L. Savard, Habitat features associated with Barrow's Goldeneye breeding in eastern Canada, 320–330
Roberts, Pauline K., see VanderWerf, Eric A. and ———
Robertson, C. J. R., P. Hyvonen, M. J. Fraser, and C. R. Pickard, Atlas of bird distribution in New Zealand 1999–2004, reviewed, 426–430
Robertson, Raleigh J., see McKinnon, Emily Anne and ———
Robin, American, see *Turdus migratorius*
Clay-colored [Thrush], see *Turdus grayi*
European, see *Erithacus rubecula*
White-throated [Thrush], see *Turdus assimilis*
Rodgiguez-Ferraro, Adriana, and Virginia Sanz, Natural history and population status of the Yellow-shouldered Parrot on La Blanquilla Island, Venezuela,
Rohe, Fabio and Andre Pinassi Antunes, Barred Forest Falcon (*Micrastur ruficollis*) predation on relatively large prey, 228–230
Rohnke, Adam T. and Ricahrd H. Yahner, Long-term effects of wastewater irrigation on habitat and a bird community in central Pennsylvania, 146–152
Rohwer, Frank C., see Baldwin, Michael J., Wylie C. Barrow Jr., Clinton Jeske, and ———
Rosas-Espinoza, Veronica Carolina, Elisa Maya-Elizarraras, Oscar Francisco Reyna Bustos, and Francisco Martin Huerta-Martinez, Diet of Acorn Woodpeckers at La Primavera Forest, Jalisco, Mexico, 494–498
Roth, Kirk L. and Kamal Islam, Habitat selection and reproductive success of Cerulean Warblers in Indiana, 105–110
Ruggera, Roman A., see Niklison, Alina M., Juan I. Areta, ———, Karie L. Decker, Carlos Bosque, and Thomas E. Martin
Ryan, Mark R., see Wells, Kimberly M. Seudkamp, Joshua J. Millspaugh, ———, and Michael W. Hubbard

S

Safine, David E. and Mark S. Lindberg, Nest habitat selection of White-winged Scoters on Yukon Flats, Alaska, 582–593
Saitoh, Takema, see Hamao, Shoji, Maria J. S. Veluz, ———, and Isao Nishiumi
Salipante, Catherine M., see Linkhart, Brian D., Erin M. Evers, Julie D. Megler, Eric C. Palm, ———, and Scott W. Yanco
Salvelinus fontinalis, 320, 322
Sanchez, Cesar, see Barrantes, Gilbert, ———, Branko Hilje, and Rodolfo Jaffe
Sandoval, Luis, Esteban Biamonte, and Alejandro Solana-Ugalde, Previously unknown food items in the diet of six neotropical bird species, 214–216
Sandpiper, Upland, see *Bartramia longicauda*
Sapsucker, Red-naped, see *Sphyrapicus nuchalis*
Yellow-bellied, see *Sphyrapicus varius*
Savard, Jean-Pierre L., see Robert, Michel, Bruno Drolet, and ———
Savard, Jean-Pierre L., see Senechal, Helene, Gilles Gauthier, and ———
Saxicola torquatus, 28, 29, 30
Schuchmann, Karl-Ludwig, see Freymann, Bernd P. and ———
Schweisinger, John, see Stromberg, Mark R., Walter D. Koenig, Eric L. Walters, and ———
Schwertner, T. Wayne, see Melton, Kyle B., Justin Z. Dreibelbis, Ray Aguirre, Bret A. Collier, ———, Markus J. Peterson, and Nova J. Silvy
Sciurotamias davidianus, 96
Scoter, species, see *Melanitta* spp.
White-winged, see *Melanitta fusca*
Scott-Morales, Laura M., see Canales-Delgadillo, Julio C., ———, Mauricio Cotera Correa, and Marisela Pando Moreno
Scytalopus magellanicus, 473
micropterus, 473, 476
parkeri, 476
schulenbergi, 475
simonsi, 473–477
superciliaris, 473, 475
Sealy, Spencer G., see Klippenstine, Dwight R. and ———
Seddon, Nathalie, see Tobias, Joseph A., Daniel J. Lebbin, Alexandre Aleixo, Michael J. Andersen, Edson Guilherme, Peter A. Hosner, and ———
Sedinger, James S., see Nicolai, Christopher A., ———, and Michael L. Wege

Seedeater, Rusty-collared, see *Sporophila collaris*
Tawny-bellied, see *Sporophila hypoxantha*
Seewagen, Chad L. and Eric J. Slayton, Mass changes of migratory landbirds during stopovers in a New York City park, 296–303
Seiurus aurocapilla, [*auricapillus*] 62, 149, 150, 151, 157, 277–285, 296–303, 446, 455–450
noveboracensis, 277–285, 296–303, 455, 458
Senechal, Helene, Gilles Gauthier, and Jean-Pierre L. Savard, Nesting ecology of Common Goldeneyes and Hooded Mergansers in a boreal river system, 732–742
Seneveratne, Sampath, see Lorenz, Stephan and ———
Servello, Frederick A., see Heath, Shane R. and ———
Setophaga ruticilla, 80, 149, 150, 151, 155, 279, 289, 291, 292, 446
Shaffer, Francois, see Dionne, Mark, Celine Maurice, Jean Gauthier, and ———
shag, see *Phalacrocorax* spp.
shearwater, see *Puffinus* spp.
Shearwater, Manx, see *Puffinus puffinus*
Sheldon, Frederick H., see Moyle, Robert G., Beth Slikas, Linda A. Whittingham, David W. Winkler, and ———
Sherry, Thomas W., see Brown, David R. and ———
Shrike, Loggerhead, see *Lanius ludovicianus*
Shultz, Christopher W., see Levad, Richard G., Kim M. Potter, ———, Carolyn Gunn, and Joseph G. Doerr
Sialia mexicana, 569, 813–819
sialis, 183, 419–422, 565–568
Silcock, Ross, review, 426–430
Silvereye, see *Zosterops lateralis*
Silvy, Nova J., see Breeden, Jeffrey B., Fidel Hernandez, Ralph L. Bingham, ———, and Gary L. Waggerman
Silvy, Nova J., see Dreibelbis, Justin Z., Kyle B. Melton, Ray Aguirre, Bret A. Collier, Jason Hardin, ———, and Markus J. Peterson
Silvy, Nova J., see Melton, Kyle B., Justin Z. Dreibelbis, Ray Aguirre, Bret A. Collier, T. Wayne Schwertner, Markus J. Peterson, and ———
Siskin, Thick-billed, see *Carduelis crassirostris*
Sitta canadensis, 142
carolinensis, 217
pusilla, 217
pygmaea, 217
spp., 692–699
Slayton, Eric J., see Seewagen, Chad L. and ———
Slikas, Beth, see Moyle, Robert G., ———, Linda A. Whittingham, David W. Winkler, and Frederick H. Sheldon
Sloan, Mark S., see Janssen, Michael H., Peter Arcese, ———, and Kelly J. Jewell
Smith, Bradley S., see Nadeau, Christopher P., Courtney J. Conway, ———, and Thomas E. Lewis
Smith, Fletcher M., see Watts, Bryan D., Michael D. Wilson, ———, Barton J. Paxton, and J. Bill Williams
snake, Chifeng beauty, see *Elaphe anomala*
eastern rat, see *Elaphe alleghaniensis*
Puerto Rican boa, see *Epicrates inornatus*
Puerto Rican racer, see *Alsophis portoricensis*
rat, see *Elaphe obsoleta*
Snow, Carter W., see Farmer, Chris, Bridget A. Frederick, Paul C. Banko, Robert M. Stephens, and ———
Snyder, Noel F. R., see Valdes-Pena, Rene A., Sonia Gabriela Ortiz-Maciel, Simon O. Valdez Juarez, Ernesto C. Enkerlin Hoeflich, and ———
Soberon, Jorge, see Menon, Shaily, Zafar-Ul, Islam, ———, and A. Townsend Peterson
Solano-Ugalde, Alejandro and Agustina Arcos-Torres, Nocturnal foraging observations of the Blue-crowned Motmot (*Momotus momota*) in San Jose, Costa Rica, 653–654
Solano-Ugalde, Alejandro, see Sandoval, Luis, Esteban Biamonte, and ———
Solitaire, Townsend's, see *Myadestes townsendi*
Sora, see *Porzana carolina*
Sparrow, Baird's, see *Ammodramus bairdii*
Black-throated, see *Amphispiza bilineata*
Coastal Plain Swamp, see *Melospiza georgiana nigrescens*
Field, see *Spizella pusilla*
Fox, see *Passerella iliaca*
Grasshopper, see *Ammodramus savannarum*
ground, see *Melozone* spp.
House, see *Passer domesticus*
Lark, see *Chondestes grammacus*
Rufous-collared, see *Zonotrichia capensis*
Savannah, see *Passerculus sandwichensis*
Seaside, see *Ammodramus maritimus*
Song, see *Melospiza melodia*
Swamp, see *Melospiza georgiana*
Vesper, see *Pooecetes gramineus*
White-crowned, see *Zonotrichia leucophrys*
White-eared Ground, see *Melozone leucotis*
Worthen's, see *Spizella wortheni*
species *nova*
from genus *Automalus,* 10–25
Togian White-eye, *Zosterops somadikartai,* 1–9
Sperry, Jinelle H., T. Luke George, and Steve Zack, Ecological factors affecting response of Dark-eyed Juncos to prescribed burning, 131–138
Sphyrapicus nuchalis, 215, 479
varius, 219, 495
Spinetail, Creamy-crested, see *Cranioleuca albicapilla*
Spiza americana, 62, 72, 111–119, 120–130, 820–829
Spizella pusilla, 111–119, 342
wortheni, 569–574
Sporophila collaris, 879–883
hypoxantha, 879–883
squirrel, flying, see *Glaucomys volans*
rock, see *Sciurotamias davidianus*
Swinhoe's striped, see *Tamiops swinhoei*
Stephens, Robert M., see Farmer, Chris, Bridget A.

Frederick, Paul C. Banko, ———, and Carter W. Snow
Stercorarius longicaudus, 88
spp., 378
Sterna caspia, 378–383
forsteri, 381
hirundo, 381
paradisaea, 381
Stonechat, see *Saxicola torquatus*
Strix nebulosa, 422
nigrolineata, 214–216
Stromberg, Mark R., Walter D. Koenig, Eric L. Walters, and John Schweisinger, Estimate of *Trichomonas gallinae*-induced mortality in Band-tailed Pigeons, upper Carmel Valley, California, winter 2006–2007, 603–606
Stubtail, Asian, see *Urosphena squameiceps*
Sturnella magna, 62, 111–119, 120–130
neglecta, 667–673
Stutchbury, Bridget J. M. and Eugene S. Morton, Recent advances in the behavioral ecology of tropical birds, 26–37
Sula nebouxii, 399
Sunarto, see Indrawan, Mochamad, Pamela C. Rasmussen, and ———
survival
of *Motacilla tschutschensis* at Cape Romanzof, Alaska, 85–91
Swallow, Barn, see *Hirundo rustica*
Cliff, see *Petrochelidon pyrrhonota*
Golden, see *Tachycineta euchrysea*
Tree, see *Tachycineta bicolor*
Violet-green, see *Tachycineta thalassina*
Swamphen, Purple, see *Porphyrio porphyrio*
Swan, Black, see *Cygnus atratus*
Swift, Black, see *Cypseloides niger*
Chimney, see *Chaetura pelagica*
Swiston, Kyle A., see Tremain, Sarah B., ———, and Daniel J. Mennill
Sykes Jr., Paul W., Lyn S. Atherton, and Rebecca L. Payne, Yellow-throated and Red-eyed vireos foraging on green anoles during migration,
Sylvia atricapilla, 210, 269, 272, 279, 433
communis, 212
Synallaxis rutilans, 18

T

Tachycineta [*Tachycinita*] *albilinea,* 31
bicolor, 422
euchrysea, 867–871
thalassina, 813–819
Taisacan, Estanislao, see Berry, Lainie and ———
Takekawa, John Y., see Ackerman, Joshua T., ———, Jill D. Bluso, Julie L. Yee, and Collin A. Eagles-Smith
Tamiops swinhoei, 96
Tapacula, Long-tailed, see *Scytalopus micropterus*
Magellanic, see *Scytalopus magellanicus*
Puna, see *Scytalopus simonsi*
White-browed, see *Scytalopus superciliaris*
Tarwater, Corey E., Predators at nests of the Western Slaty Antshrike, (*Thamnophilus atrinucha*), 620–624
taxonomy
of *Cettia seebohmi* and *Cettia diphone,* 268–276
Teal, Chestnut, see *Anas castanea*
Cinnamon, see *Anas cyanoptera*
Tegu, Black-white, see *Tupinambis merianae*
Terenura maculata, 20
sicki, 20
Tern, Arctic, see *Sterna paradisaea*
Black, see *Chlidonias niger*
Caspian, see *Sterna caspia*
Common, see *Sterna hirundo*
Forster's, see *Sterna forsteri*
Thamnophilus atrinucha, 620–624
Thrasher, Bendire's, see *Toxostoma bendirei*
Brown, see *Toxostoma rufum*
Curve-billed, see *Toxostoma curvirostra*
LeConte's, see *Toxostoma lecontei*
Pearly-eyed, see *Margarops fuscatus*
Thrush, Bicknell's, see *Catharus bicknelli*
Blue Rock, see *Monticola solitarius*
Clay-colored, see *Turdus grayi*
Great, see *Turdus fuscater*
Hermit, see *Catharus guttatus*
Pale-breasted, *Turdus leucomelas*
Red-legged, see *Turdus plumbeus*
Rufous-bellied, see *Turdus rufiventris*
Song, see *Turdus philomelos*
Sooty, see *Turdus nigrescens*
Swainson's, see *Catharus ustulatus*
White-throated, see *Monticola gularis*
Wood, see *Hylocichla mustelina*
Thryothorus euophrys, 34
fasciatoventris, 34
leucotis, 31, 33, 34
ludovicianus, 467–472
rufalbus, 34
Tinamou, Brown, see *Crypturellus obsoletus*
Tit, Great, see *Parus major*
Marsh, see *Poecile palustris*
Willow, see *Poecile montana*
Tit-spinetail, Andean, see *Leptasthenura andicola*
Tawny, see *Leptasthenura yanacensis*
White-browed, see *Leptasthenura xenothorax*
Tit-Tyrant, Ash-breasted, see *Anairetes alpinus*
Tufted, see *Anairetes parulus*
Titanohierax gloveralleni,
Titman, Rodger D., see Craik, Shawn R. and ———
Titmouse, Tufted, see *Baeolophus bicolor*
Tobias, Joseph A., Daniel J. Lebbin, Alexandre Aleixo, Michael J. Andersen, Edson Guilherme, Peter A. Hosner and Nathalie Seddon, Distribution, behavior, and conservation status of the Rufous Twistwing (*Cnipodectes superrufus*), 38–49
Tomasevic, Jorge A., Estades, Cristian, M. Angelica Vukasovic, and ———
tortoise, Aldabra giant, see *Dipsochelys dussumieri*
Tossas, Adrianne G., Reproductive success of the Puerto Rican Vireo in montane habitat, 460–466

Towhee, California, see *Pipilo crissalis*
Eastern, see *Pipilo erythrophthalmus*
Spotted, see *Pipilo maculatus*
Townsend, Jason M., Esteban Garrido, and Danilo A. Mejia, Nests and nesting behavior of Golden Swallow (*Tachycineta euchrysea*) in abandoned bauxite mines in the Dominican Republic, 867–871
Toxostoma bendirei, 342
curvirostre, 342
lecontei, 342
rufum, 343
Tozer, Douglas C., Nests of Black-throated Green Warblers in tree cavities, 409–412
Tremain, Sarah B., Kyle A. Swiston, and Daniel J. Mennill, Seasonal variation in acoustic signals of Pileated Woodpeckers, 499–504
Troglodytes aedon, 99–104, 216
troglodytes, 155, 287
Trogon, Amazon White-tailed, see *Trogon viridis*
Bare-cheeked, see *Apaloderma aequatoriale*
Black-headed, see *Trogon melanocephalus*
Choco, see *Trogon comptus*
Citreoline, see *Trogon citreolus*
Hispaniolan, see *Priotelus roseigster*
Narina, see *Apaloderma narina*
Slaty-tailed, see *Trogon massena*
Violaceous, see *Trogon violaceus*
Trogon citreolus, 249
comptus, 249
massena, 249
melanocephalus, 248–255
violaceus, 249
viridis, 249
trout, brook, see *Salvelinus fontinalis*
Trudell, Heidi, see Hager, Stephen B., ———, Kelly J. McKay, Stephanie M. Crandall, and Lance Mayer
Tupinambis merianae, 229
Turdus assimilis, 62
fuscater, 28
grayi, 28, 31, 32, 214–216
merula, 209
migratorius, 146–152, 209–213, 297, 525–530
nigrescens, 214–216
philomelos, 350
plumbeus, 464
rufiventris, 27
Turkey, Ocellated, see *Meleagris ocellata*
Wild, see *Meleagris gallopavo*
Twistwing, Brownish, see *Cnipodectes subbruneus*
Rufous, see *Cnipodectes superrufus*
Tympanuchus cupido, 129
Tyrannus dominicensis, 655–657
tyrannus, 287
Tyto soumagnei, 891–897

U

Uria aalge, 635–636
Urocissa erythrorhyncha, 96
Urosphena squameiceps, 269, 272
Uyehara, Kimberly J., Andrew Engilis Jr., and Bruce D. Dugger, Wetland features that influence occupancy by the endangered Hawaiian Duck, 311–319

V

Valdes-Pena, Rene A., Sonia Gabriela Ortiz-Maciel, Simon O. Valdez Juarez, Ernesto C. Enkerlin Hoeflich, and Noel F. R. Snyder, Use of clay licks by Maroon-fronted Parrots (*Rhynchopsitta terrisi*) in northern Mexico, 176–180
Vanderhoff, E. Natasha and Perri K. Eason, Comparisons between juvenile and adult American Robins foraging for mulberry fruit, 209–213
VanderWerf, Eric A. and Pauline K. Roberts, Foraging and nesting of the Akikiki or Kauai Creeper (*Oreomystis bairdi*), 195–199
Veery, see *Catharus fuscescens*
Veluz, Maria J. S., see Hamao, Shoji, ———, Takema Saitoh, and Isao Nishiumi
Vermivora chrysoptera, 366–370, 801–812
peregrina, 278
pinus, 366–370
Vilella, Francisco J., see Wood, Douglas R., ———, and L. Wesley Burger Jr.
Violetear, Green, see *Colibri thalassinus*
Sparkling, see *Colibri coruscans*
White-vented, see *Colibri serrirostris*
Vireo altiloquus, 460
atricapilla, 407–409
gilvus, 297
griseus, 286–295
huttoni, 478
latimeri, 460–466
olivaceus, 146–152, 157, 277–285, 286–295, 897–900
solitarius, 155, 287
Vireo, Black-capped see *Vireo atricapilla*
Black-whiskered, see *Vireo altiloquus*
Blue-headed, see *Vireo solitarius*
Hutton's, see *Vireo huttoni*
Red-eyed, see *Vireo olivaceus*
Warbling, see *Vireo gilvus*
White-eyed, see *Vireo griseus*
vocalization
begging behavior of *Cacomantis sepulcralis,* 887–890
communal calling and prospecting by *Trogon melanocephalus,* 248–255
difference between *Cettia seebohmi* and *Cettia diphone,* 268–276
male song variation of *Colibri thalassinus* in the Talmanca Mountain Range, Costa Rica, 519–524
of *Mimus polyglottos,* 717–724
seasonal variation in *Dryocopus pileatus,* 499–504
song variation in *Empidonax fulvifrons,* 256–267
type B song of *Dendroica dominica,* 401–403
Volatinia jacarina, 31, 32, 398
von Wehrden, Henrik, The Giant Hummingbird (*Patagona gigas*) in the mountains of central Argen-

tina and a climatic envelope model for its distribution, 648–651
Vukasovic, M. Angelica, see Estades, Cristian, ———, and Jorge A. Tomasevic
Vulpes vulpes, 88

W

Waggerman, Gary L., see Breeden, Jeffrey B., Fidel Hernandez, Ralph L. Bingham, Nova J. Silvy, and ———
Wagtail, Eastern Yellow, see *Motacilla tschutschensis*
Western Yellow, see *Motacilla flava*
White, see *Motacilla alba*
Walters, Eric L., see Stromberg, Mark R., Walter D. Koenig, ———, and John Schweisinger
Wang, Ning, Yanyun Zhang, and Guangmei Zheng, Breeding ecology of the Narcissus Flycatcher in north China, 92–98
Wang, Qiang and Feng Li, Nest raising by Red-crowned Cranes in response to human-mediated flooding at Zhalong Nature Reserve, China, 610–613
Wanless, Ross M. and Philip A. R. Hockey, Natural history and behavior of the Aldabra Rail (*Dryolimnas* [*cuvieri*] *aldabranus*), 50–61
Warbler, Arctic, see *Phylloscopus borealis*
Black-throated Blue, see *Dendroica caerulescens*
Black-throated Green, see *Dendroica virens*
Blue-winged, see *Vermivora pinus*
Canada, see *Wilsonia canadensis*
Cape May, see *Dendroica tigrina*
Cerulean, see *Dendroica cerulea*
Cetti's, see *Cettia cetti*
Chestnut-sided, see *Dendroica pensylvanica*
Golden-winged, see *Vermivora chrysoptera*
Great Reed, see *Acrocephalus arundinaceus*
Green-tailed, see *Microligea palustris*
Hooded, see *Wilsonia citrina*
Japanese Bush, see *Cettia diphone*
Kentucky, see *Oporornis formosus*
MacGillivray's, see *Oporornis tolmiei*
Magnolia, see *Dendroica magnolia*
Oriental Reed, see *Acrocephalus arientalis*
Philippine Bush, see *Cettia seebohmi*
Pine, see *Dendroica pinus*
Prairie, see *Dendroica discolor*
Prothonotary, see *Protonotaria citrea*
Swainson's, see *Limnothlypis swainsonii*
Tennessee, see *Vermivora peregrina*
Willow, see *Phylloscopus trochilus*
Wilson's, see *Wilsonia pusilla*
Worm-eating, see *Helmitheros vermivorum* [*vermivorus*]
Yellow, see *Dendroica petechia*
Yellow-rumped, see *Dendroica coronata*
Yellow-throated, see *Dendroica dominica*
Waterthrush, Northern, see *Seiurus noveboracensis*
Watts, Bryan D., Michael D. Wilson, Fletcher M. Smith, Barton J. Paxton, and J. Bill Williams, Breeding range extension of the Coastal Plain Swamp Sparrow, 393–395
Watts, Bryan D., see Wilson, Michael D. and ———
Waxwing, Cedar, see *Bombycilla cedrorum*
Weakley Jr., Leonard, see Oehler, David A., Steve Pelikan, W. Roger Fry, ———, Alejandro Kusch, and Manuel Marin
weasel, see *Mustela* spp.
Siberian, see *Mustela gularis*
Wege, Michael L., see Nicolai, Christopher A., James S. Sedinger, and ———
Wells, Kimberly M. Suedkamp, Joshua J. Millspaugh, Mark R. Ryan, and Michael W. Hubbard, Factors affecting home range size and movements of post-fledging grassland birds, 120–130
Wetzel, Daniel P. and C. Ray Chandler, Adoption: adaptation or reproductive error in Eastern Bluebirds, 419–422
Wheatear, Northern, see *Oenanthe oenanthe*
Wheeler, Brian K., Raptors of eastern [western] North America, reviewed, 430–431
White, Jennifer D. and John Faaborg, Post-fledging movement and spatial habitat-use patterns of juvenile Swainson's Thrushes, 62–73
Whip-poor-will, see *Caprimulgus vociferus*
Whitaker, S. J., see Fair, J. M. and ———
White-eye, Black-crowned, see *Zosterops atrifrons*
Everett's, see *Zosterops everetti*
Lemon-bellied, see *Zosterops chloris*
Mountain, see *Zosterops montanus*
Pale-bellied, see *Zosterops consobrinorum*
Rota, see *Zosterops rotensis*
Sanghie, see *Zosterops nehrkorni*
Seram, see *Zosterops stalkeri*
Togian, see *Zosterops somadikartai*
Whitethroat, Common, see *Sylvia communis*
Whittingham, Linda A., see Moyle, Robert G., Beth Slikas, ———, David W. Winkler, and Frederick H. Sheldon
Wilson, Amy G., see Wilson, Scott, Keith A. Hobson, Douglas M. Collister, and ———
Wilson, J. Bill, see Watts, Bryan D., Michael D. Wilson, Fletcher M. Smith, Barton J. Paxton, and ———
Wilson, Michael D. and Bryan D. Watts, Landscape configuration effects on distribution and abundance of Whip-poor-wills, 778–783
Wilson, Michael D., see Watts, Bryan D., ———, Fletcher M. Smith, Barton J. Paxton, and J. Bill Williams
Wilson, Robert E. and Kevin G. McCracken, Specimen shrinkage in Cinnamon Teal, 390–392
Wilson, Scott, Keith A. Hobson, Douglas M. Collister, and Amy G. Wilson, Spring migratory stopover of Swainson's Thrush along the Pacific coast of southwest Costa Rica, 74–84
Wilson, William J., Use of legs and feet for control by scoters during aerial courtship, 594–599
Wilsonia canadensis, 155
citrina, 62, 277–285, 291, 342, 370
pusilla, 288
Winker, Kevin and Gary R. Graves, Genetic structure

of breeding and wintering populations of Swainson's Warbler, 433–445
Winker, Kevin, see Johnson, Andrew B. and ———
Winkler, David W., see Moyle, Robert G., Beth Slikas, Linda A. Whittingham, ———, and Frederick H. Sheldon
Wood, Douglas R., Francisco J. Vilella, and L. Wesley Burger Jr., Red-cockaded Woodpecker home range use and the macrohabitat selection in a loblolly-shortleaf pine forest, 793–800
Wood, Petra Bohall, see Ammer, Frank K., ———, and Roger J. McPherson
Wood-Pewee, Eastern, see *Contopus virens*
Western, see *Contopus sordidulus*
Woodpecker, Acorn, see *Melanerpes formicivorus*
Arizona, see *Picoides arizonae*
Cuban Green, see *Xiphidiopicus percussus*
Downy, see *Picoides pubescens*
Gray-breasted, see *Melanerpes hypopolius*
Great Spotted, see *Dendrocopus* [*Picoides*] *major*
Hairy, see *Picoides villosus*
Hoffmann's, see *Melanerpes hoffmanni*
Ladder-backed, see *Picoides scalaris*
Lesser Spotted, see *Dendrocopos minor*
Lewis's, see *Melanerpes lewis*
Middle Spotted, see *Dendrocopos medius*
Pileated, see *Dryocopus pileatus*
Plain-tailed, see *Thryothorus euophrys*
Red-bellied, see *Melanerpes carolinus*
Red-cockaded, see *Picoides borealis*
Red-headed, see *Melanerpes erythrocephalus*
Syrian, see *Dendrocopus syriacus*
White-backed, see *Dendrocopus leucotos*
White-headed, see *Picoides albolarvatus*
Yellow-fronted, see *Melanerpes flavifrons*
Woods, Christopher P. and R. Mark Brigham, Common Poorwill activity and calling behavior in relation to moonlight and predation, 505–512
Woolaver, Lance G., see Rimmer, Christopher C., ———, Rina K. Nichols, Eladio M. Fernandez, Steven C. Latta, and Esteban Garrido
Wren, Black-bellied, see *Thryothorus fasciatoventris*
Buff-breasted, see *Thryothorus leucotis*
Carolina, see *Thryothorus ludovicianus*
House, see *Troglodytes aedon*
Rufous-and-white, see *Thryothorus rufalbus*
Winter, see *Troglodytes troglodytes*
Wunker, Elizabeth H., see Cohen, Jonathan B., ———, and James D. Fraser

X

Xanthocephalus xanthocephalus, 342, 657–659
Xenodacnis parina, 531–544
Xenoligea montana, 190–195
Xiphidiopicus percussus, 215

Y

Yahner, Richard H., Bird responses to a managed forested landscape, 897–900
Yahner, Richard H., see Kubel, Jacob E. and ———
Yahner, Richard H., see Rohnke, Adam T. and ———
Yanco, Scott W., see Linkhart, Brian D., Erin M. Evers, Julie D. Megler, Eric C. Palm, Catherine M. Salipante, and ———
Yaukey, Peter H. and Shawn C. Powell, Numbers of migratory birds stopping over in New Orleans, Louisiana, USA in relation to weather, 286–295
Yee, Julie L., see Ackerman, Joshua T., John Y. Takekawa, Jill D. Bluso, ———, and Collin A. Eagles-Smith
Yellowthroat, Common, see *Geothlypis trichas*
Yom-Tov, Yoram, see Leader, Zohar, ———, and Uzi Motro
York, Matthew W., review, 236–237
Yuehua, Sun, see Chenxi, Jia and ———

Z

Zack, Steve, see Sperry, Jinelle H., T. Luke George, and ———
Zalik, Nathan J. and Noah G. Perlut, Simultaneous incubation by two females and nestling provisioning by four adults at a Savanna Sparrow nest, 628–630
Zenaida asiatica, 384–389
macroura, 149
Zhang, Yanyun, see Wang, Ning, ———, and Guangmei Zheng
Zheng, Guangmei, see Wang, Ning, Yanyun Zhang, and ———
Zimmer, Kevin J., The White-Eyed Foliage-gleaner (Funariidae: *Automolus*) is two species, 10–25
Zimmerman, Guthrie S., Rick R. Horton, Daniel R. Dessecker, and R. J. Gutierrez, New insight to old hypotheses: Ruffed Grouse population cycles, 239–247
Zonotrichia capensis, 30, 31
leucophrys, 30
Zosterops anomalus, 1, 3, 7
atrifrons, 1–9
chloris, 1
consobrinorum, 1, 2
everetti, 1
lateralis, 31
montanus, 1
nehrkorni, 1, 3, 5
rotensis, 618–619
somakidartai, 1–9, (Frontispiece)
stalkeri, 1

The Wilson Journal *of Ornithology*

Published by the Wilson Ornithological Society

Volume 120 *2008* *Quarterly*

EDITOR: CLAIT E. BRAUN
EDITORIAL BOARD: RICHARD C. BANKS
KATHY G. BEAL
JACK CLINTON EITNIEAR
SARA J. OYLER-McCANCE
REVIEW EDITOR: MARY GUSTAFSON
INDEX EDITOR: KATHY G. BEAL
EDITORIAL ASSISTANT: NANCY J. K. BRAUN

The Wilson Ornithological Society

Founded 3 December 1888

Named after ALEXANDER WILSON, the first American Ornithologist

President—James D. Rising, Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada; e-mail: rising@zoo.utoronto.ca

First Vice-President—E. Dale Kennedy, Biology Department, Albion College, Albion, MI 49224, USA; e-mail: dkennedy@albion.edu

Second Vice-President—Robert C. Beason, USDA, Wildlife Services, 6100 Columbus Avenue, Sandusky, OH 44870, USA; e-mail: beason@netzero.com

Editor—Clait E. Braun, 5572 North Ventana Vista Rd., Tucson, AZ 85750, USA; e-mail: TWILSONJO@comcast.net

Secretary—John A. Smallwood, Department of Biology and Molecular Biology, Montclair State University, Montclair, NJ 07043, USA; e-mail: smallwood@montclair.edu

Treasurer—Melinda M. Clark, 52684 Highland Drive, South Bend, IN 46635, USA; e-mail: MClark@tcservices.biz

Elected Council Members— Carla J. Dove, Greg H. Farley, and Mia R. Revels (terms expire 2009); Rebecca Holberton, Robert S. Mulvihill, and Timothy O'Connell (terms expire 2010); Jameson F. Chace, Sara R. Morris, and Margaret A. Voss (terms expire 2011).

DATES OF ISSUE OF VOLUME 120 OF

THE WILSON JOURNAL OF ORNITHOLOGY

NO. 1—12 MARCH 2008
NO. 2—28 MAY 2008
NO. 3—5 SEPTEMBER 2008
NO. 4—31 DECEMBER 2008

CONTENTS OF VOLUME 120

NUMBER 1

Major Articles

1 A new White-eye (*Zosterops*) from the Togian Islands, Sulawesi, Indonesia
Mochamad Indrawan, Pamela C. Rasmussen, and Sunarto

10 The White-eyed Foliage-gleaner (Furnariidae: *Automolus*) is two species
Kevin J. Zimmer

26 Recent advances in the behavioral ecology of tropical birds
Bridget J. M. Stutchbury and Eugene S. Morton

38 Distribution, behavior, and conservation status of the Rufous Twistwing (*Cnipodectes superrufus*)
Joseph A. Tobias, Daniel J. Lebbin, Alexandre Aleixo, Michael J. Andersen, Edson Guilherme, Peter A. Hosner, and Nathalie Seddon

50 Natural history and behavior of the Aldabra Rail (*Dryolimnas* [*cuvieri*] *aldabranus*)
Ross M. Wanless and Philip A. R. Hockey

62 Post-fledging movement and spatial habitat-use patterns of juvenile Swainson's Thrushes
Jennifer D. White and John Faaborg

74 Spring migratory stopover of Swainson's Thrush along the Pacific Coast of southwest Costa Rica
Scott Wilson, Keith A. Hobson, Douglas M. Collister, and Amy G. Wilson

85 Demography of Eastern Yellow Wagtails at Cape Romanzof, Alaska
Heather M. Renner and Brian J. McCaffery

92 Breeding ecology of the Narcissus Flycatcher in north China
Ning Wang, Yanyun Zhang, and Guangmei Zheng

99 Reproductive success of House Wrens in suburban and rural landscapes
Michael J. Newhouse, Peter P. Marra, and L. Scott Johnson

105 Habitat selection and reproductive success of Cerulean Warblers in Indiana
Kirk L. Roth and Kamal Islam

111 Nesting biology of grassland birds at Fort Campbell, Kentucky and Tennessee
James J. Giocomo, E. Daniel Moss, David A. Buehler, and William G. Minser

120 Factors affecting home range size and movements of post-fledging grassland birds
Kimberly M. Suedkamp Wells, Joshua J. Millspaugh, Mark R. Ryan, and Michael W. Hubbard

131 Ecological factors affecting response of Dark-eyed Juncos to prescribed burning
Jinelle H. Sperry, T. Luke George, and Steve Zack

139 Winter habitat use by Boreal Chickadee flocks in a managed forest
Adam Hadley and André Desrochers

146 Long-term effects of wastewater irrigation on habitat and a bird community in central Pennsylvania
Adam T. Rohnke and Richard H. Yahner

153 Long-term trends in breeding birds in an old-growth Adirondack forest and the surrounding region
Stacy A. McNulty, Sam Droege, and Raymond D. Masters

159 Timing and location of mortality of fledgling, subadult, and adult California Gulls
Bruce H. Pugesek and Kenneth L. Diem

167 Effects of predation and food provisioning on Black Tern chick survival
Shane R. Heath and Frederick A. Servello

176 Use of clay licks by Maroon-fronted Parrots (*Rhynchopsitta terrisi*) in northern Mexico
Rene A. Valdés-Peña, Sonia Gabriela Ortiz-Maciel, Simon O. Valdez Juarez, Ernesto C. Enkerlin Hoeflich, and Noel F. R. Snyder

181 Cavity number and use by other species as correlates of group size in Red-cockaded Woodpeckers
John J. Kappes Jr.

Short Communications

190 First description of nests and eggs of two Hispaniolan endemic species: Western Chat-tanager (*Calyptophilus tertius*) and Hispaniolan Highland-tanager (*Xenoligea montana*)
Christopher C. Rimmer, Lance G. Woolaver, Rina K. Nichols, Eladio M. Fernández, Steven C. Latta, and Esteban Garrido

195 Foraging and nesting of the 'Akikiki or Kaua'i Creeper (*Oreomystis bairdi*)
Eric A. VanderWerf and Pauline K. Roberts

200 First observation of duetting in the Olive-backed Euphonia (*Euphonia gouldi*)
Thor Hanson

201 The display of a Reddish Hermit (*Phaethornis ruber*) in a lowland rainforest, Bolivia
Adam Felton, Annika M. Felton, and David B. Lindenmayer

205 Home range and habitat preferences of the Banded Ground-cuckoo (*Neomorphus radiolosus*)
Jordan Karubian and Luis Carrasco

209 Comparisons between juvenile and adult American Robins foraging for mulberry fruit
E. Natasha Vanderhoff and Perri K. Eason

214 Previously unknown food items in the diet of six neotropical bird species
Luis Sandoval, Esteban Biamonte, and Alejandro Solano-Ugalde

217 Anvil use by the Red-cockaded Woodpecker
Kristin J. Bondo, Lauren N. Gilson, and Reed Bowman

221 Gender identification of Grasshopper Sparrows comparing behavioral, morphological, and molecular techniques
Frank K. Ammer, Petra Bohall Wood, and Roger J. McPherson

226 Abnormal eggs of Rio Grande Wild Turkeys on the Edwards Plateau, Texas
Kyle B. Melton, Justin Z. Dreibelbis, Ray Aguirre, Bret A. Collier, T. Wayne Schwertner, Markus J. Peterson, and Nova J. Silvy

228 Barred Forest Falcon (*Micrastur ruficollis*) predation on relatively large prey
Fábio Röhe and André Pinassi Antunes

231 Ornithological Literature
Compiled by Mary Gustafson

237 Editor's Comments

NUMBER 2

Major Articles

239 New insight to old hypotheses: Ruffed Grouse population cycles
Guthrie S. Zimmerman, Rick R. Horton, Daniel R. Dessecker, and R. J. Gutiérrez

248 Communal calling and prospecting by Black-headed Trogons (*Trogon melanocephalus*)
Christina Riehl

256 Song variation in Buff-breasted Flycatchers (*Empidonax fulvifrons*)
M. Ross Lein

268 Phylogenetic relationship and song differences between closely related Bush Warblers (*Cettia seebohmi* and *C. diphone*)
Shoji Hamao, Maria J. S. Veluz, Takema Saitoh, and Isao Nishiumi

277 Autumn stopover near the Gulf of Honduras by Nearctic-Neotropic migrants
Andrew B. Johnson and Kevin Winker

286 Numbers of migratory birds stopping over in New Orleans, Louisiana, USA in relation to weather
Peter H. Yaukey and Shawn C. Powell

296 Mass changes of migratory landbirds during stopovers in a New York City park
Chad L. Seewagen and Eric J. Slayton

304 Migration of Florida sub-adult Bald Eagles
Elizabeth K. Mojica, J. Michael Meyers, Brian A. Millsap, and Katherin L. Haley

311 Wetland features that influence occupancy by the endangered Hawaiian Duck
Kimberly J. Uyehara, Andrew Engilis Jr., and Bruce D. Dugger

320 Habitat features associated with Barrow's Goldeneye breeding in eastern Canada
Michel Robert, Bruno Drolet, and Jean-Pierre L. Savard

331 Distribution, abundance, and nest-site characteristics of Black Swifts in the southern Rocky Mountains of Colorado and New Mexico
Richard G. Levad, Kim M. Potter, Christopher W. Shultz, Carolyn Gunn, and Joseph G. Doerr

339 Nest reuse by Vermilion Flycatchers in Texas
Kevin S. Ellison

345 Natural history and breeding biology of the Rusty-breasted Antpitta (*Grallaricula ferrugineipectus*)
Alina M. Niklison, Juan I. Areta, Roman A. Ruggera, Karie L. Decker, Carlos Bosque, and Thomas E. Martin

353 Foraging ecology of parrots in a modified landscape: seasonal trends and introduced species
Greg D. Matuzak, M. Bernadette Bezy, and Donald J. Brightsmith

366 The signal function of a melanin-based plumage ornament in Golden-winged Warblers
Emily Anne McKinnon and Raleigh J. Robertson

371 Factors influencing fidelity of House Finches to a feeding station
Andrew K. Davis

378 Gender identification of Caspian Terns using external morphology and discriminant function analysis
Joshua T. Ackerman, John Y. Takekawa, Jill D. Bluso, Julie L. Yee, and Collin A. Eagles-Smith

384 Effects of traffic noise on auditory surveys of urban White-winged Doves
Jeffrey B. Breeden, Fidel Hernández, Ralph L. Bingham, Nova J. Silvy, and Gary L. Waggerman

Short Communications

390 Specimen shrinkage in Cinnamon Teal
Robert E. Wilson and Kevin G. McCracken

393 Breeding range extension of the Coastal Plain Swamp Sparrow
Bryan D. Watts, Michael D. Wilson, Fletcher M. Smith, Barton J. Paxton, and J. Bill Williams

395 Polyandry and sex ratio in the Song Sparrow
Michael H. Janssen, Peter Arcese, Mark S. Sloan, and Kelly J. Jewell

398 Novel courtship behavior in the Little Greenbul (*Andropadus virens*)
Alexander N. G. Kirschel

401 A recording of a Type B song of the Yellow-throated Warbler
Bailey D. McKay

404 Substrate and vegetation selection by nesting Piping Plovers
Jonathan B. Cohen, Elizabeth H. Wunker, and James D. Fraser

407 Nest site selection by a male Black-capped Vireo
Andrew J. Campomizzi, Shannon L. Farrell, and Jerrod A. Butcher

409 Nests of Black-throated Green Warblers in tree cavities
Douglas C. Tozer

413 Nests and fledglings of the Red-ruffed Fruitcrow (*Pyroderus scutatus*)
Mercival R. Francisco, Paulo R. R. Oliveira Jr., and Vitor O. Lunardi

416 Palila (*Loxioides bailleui*) fledgling fed by Hawai'i 'Amakihi (*Hemignathus virens*)
Chris Farmer, Bridget A. Frederick, Paul C. Banko, Robert M. Stephens, and Carter W. Snow

419 Adoption: adaptation or reproductive error in Eastern Bluebirds?
Daniel P. Wetzel and C. Ray Chandler

422 An intraspecific killing in adult Pacific Reef Egrets (*Egretta sacra*)
Christa Beckmann

425 Ornithological Literature
Compiled by Mary Gustafson

NUMBER 3

Major Articles

433 Genetic structure of breeding and wintering populations of Swainson's Warbler
Kevin Winker and Gary R. Graves

446 Does age influence territory size, habitat selection, and reproductive success of male Canada Warblers in central New Hampshire?
Leonard R. Reitsma, Michael T. Hallworth, and Phred M. Benham

455 Solitary winter roosting of Ovenbirds in core foraging area
David R. Brown and Thomas W. Sherry

460 Reproductive success of the Puerto Rican Vireo in a montane habitat
Adrianne G. Tossas

467 Nest defense by Carolina Wrens
Kelly A. D'Orazio and Diane L. H. Neudorf

473 Nests, eggs, and parental care of the Puna Tapaculo (*Scytalopus simonsi*)
Peter A. Hosner and Noemí E. Huanca

478 Phylogeographic patterns of differentiation in the Acorn Woodpecker
Magali Honey-Escandón, Blanca E. Hernández-Baños, Adolfo G. Navarro-Sigüenza, Hesiquio Benítez-Díaz, and A. Townsend Peterson

494 Diet of Acorn Woodpeckers at La Primavera Forest, Jalisco, Mexico
Veronica Carolina Rosas-Espinoza, Elisa Maya-Elizarraras, Oscar Francisco Reyna Bustos, and Francisco Martin Huerta-Martinez

499 Seasonal variation in acoustic signals of Pileated Woodpeckers
Sarah B. Tremain, Kyle A. Swiston, and Daniel J. Mennill

505 Common Poorwill activity and calling behavior in relation to moonlight and predation
Christopher P. Woods and R. Mark Brigham

513 Maximizing detection probability of wetland-dependent birds during point-count surveys in northwestern Florida
Christopher P. Nadeau, Courtney J. Conway, Bradley S. Smith, and Thomas E. Lewis

519 Male song variation of Green Violetear (*Colibri thalassinus*) in the Talamanca Mountain Range, Costa Rica
Gilbert Barrantes, César Sánchez, Branko Hilje, and Rodolfo Jaffé

525 Metabolizable energy in Chinese Tallow fruit for Yellow-rumped Warblers, Northern Cardinals, and American Robins
Michael J. Baldwin, Wylie C. Barrow Jr., Clinton Jeske, and Frank C. Rohwer

531 Foraging ecology of High Andean insectivorous birds in remnant *Polylepis* forest patches
Huw Lloyd

545 Nesting biology of the Giant Conebill (*Oreomanes fraseri*) in the High Andes of Bolivia
J. R. A. Cahill, E. Matthysen, and N. E. Huanca

550 Bird density and mortality at windows
Stephen B. Hagar, Heidi Trudell, Kelly J. McKay, Stephanie M. Crandall, and Lance Mayer

565 Ectoparasites affect hemoglobin and percentages of immature erythrocytes but not hematocrit in nestling Eastern Bluebirds
Reneé E. Carleton

569 Observations on flocking behavior of Worthen's Sparrow (*Spizella wortheni*) and occurrence in mixed-species flocks
Julio C. Canales-Delgadillo, Laura M. Scott-Morales, Mauricio Cotera Correa, and Marisela Pando Moreno

575 Status of Crested Penguin (*Eudyptes* spp.) populations on three islands in southern Chile
David A. Oehler, Steve Pelikan, W. Roger Fry, Leonard Weakley Jr., Alejandro Kusch, and Manuel Marin

582 Nest habitat selection of White-winged Scoters on Yukon Flats, Alaska
David E. Safine and Mark S. Lindberg

Short Communications

594 Use of legs and feet for control by scoters during aerial courtship
William J. Wilson

599 Bill entanglement in subcutaneously-anchored radio transmitters on Harlequin Ducks
Jeanine Bond and Daniel Esler

603 Estimate of *Trichomonas gallinae*-induced mortality in Band-tailed Pigeons, upper Carmel Valley, California, winter 2006-2007
Mark R. Stromberg, Walter D. Koenig, Eric L. Walters, and John Schweisinger

606 Winter ecology of Yellow Rails based on South Carolina specimens
William Post

610 Nest raising by Red-crowned Cranes in response to human-mediated flooding at Zhalong Nature Reserve, China
Qiang Wang and Feng Li

613 White-winged Diuca Finch (*Diuca speculifera*) nesting on Quelccaya Ice Cap, Perú
Douglas R. Hardy and Spencer P. Hardy

618 Nest success and nest predation of the endangered Rota White-eye (*Zosterops rotensis*)
Lainie Berry and Estanislao Taisacan

620 Predators at nests of the Western Slaty Antshrike (*Thamnophilus atrinucha*)
Corey E. Tarwater

625 Evidence for Bachman's Sparrow raising Brown-headed Cowbirds to fledging
Matthew J. Reetz, Elizabeth Farley, and Thomas A. Contreras

628 Simultaneous incubation by two females and nestling provisioning by four adults at a Savannah Sparrow nest
Nathan J. Zalik and Noah G. Perlut

631 Grey Heron (*Ardea cinerea*) predation on the Aldabra White-throated Rail (*Dryolimnas cuvieri aldabranus*)
Pierre A. Pistorius

633 Purple Swamphens (*Porphyrio porphyrio*) attempting to prey upon Black Swan (*Cygnus atratus*) eggs and preying upon a cygnet on an urban lake in Melbourne, Australia
Shandiya Balasubramaniam and Patrick-Jean Guay

635 Northern Fulmar predation of Common Murre
Stephan Lorenz and Sampath Seneveratne

637 Diet of nestling Black-crowned Night-herons in a mixed species colony: implications for Tern conservation
C. Scott Hall and Stephen W. Kress

641 Diet of the Long-eared Owl in the northern and central Negev Desert, Israel
Zohar Leader, Yoram Yom-Tov, and Uzi Motro

645 First observed instance of polygyny in Flammulated Owls
Brian D. Linkhart, Erin M. Evers, Julie D. Megler, Eric C. Palm, Catherine M. Salipante, and Scott W. Yanco

648 The Giant Hummingbird (*Patagona gigas*) in the mountains of central Argentina and a climatic envelope model for its distribution
Henrik von Wehrden

651 Giant Hummingbirds (*Patagona gigas*) ingest calcium-rich minerals
Cristián F. Estades, M. Angélica Vukasovic, and Jorge A. Tomasevic

654 Nocturnal foraging observations of the Blue-crowned Motmot (*Momotus momota*) in San José, Costa Rica
Alejandro Solano-Ugalde and Agustina Arcos-Torres

655 Kleptoparasitism by Grey Kingbirds (*Tyrannus dominicensis*) in Barbados
Sarah E. Overington, Laure Cauchard, and Kimberly-Ann Côté

657 Double-scratching by Yellow-headed Blackbirds
Alan de Queiroz

660 **Ornithological Literature**
Compiled by Mary Gustafson and Clait E. Braun

NUMBER 4

Major Articles

667 Differential ejection of cowbird eggs and non-mimetic eggs by grassland Passerines
Dwight R. Klippenstine and Spencer G. Sealy

674 Between and within clutch variation of egg size in Greater Rheas
Gustavo J. Fernández and Juan C. Reboreda

683 DNA sequence assessment of phylogenetic relationships among New World martins (Hirundinidae: *Progne*)
Robert G. Moyle, Beth Slikas, Linda A. Whittingham, David W. Winkler, and Frederick H. Sheldon

692 Preliminary analysis of the ecology and geography of the Asian nuthatches (Aves: Sittidae)
Shaily Menon, Zafar-ul Islam, Jorge Soberón, and A. Townsend Peterson

700 Density and abundance of Mountain Plovers in northeastern Montana
Theresa M. Childers and Stephen J. Dinsmore

708 Land cover associations of nesting territories of three sympatric *Buteo*s in shortgrass prairie
Scott McConnell, Timothy J. O'Connell, and David M. Leslie Jr.

717 Species recognition in a vocal mimic: repetition pattern not the only cue used by Northern Mockingbirds in discriminating songs of conspecifics and Brown Thrashers
Dustin G. Reichard and J. Jordan Price

725 Lesser Snow Geese and Ross's Geese form mixed flocks during winter but differ in family maintenance and social status
Jón Einar Jónsson and Alan D. Afton

732 Nesting ecology of Common Goldeneyes and Hooded Mergansers in a boreal river system
Hélène Sénéchal, Gilles Gauthier, and Jean-Pierre L. Savard

743 Movements and habitat use by Red-breasted Merganser broods in eastern New Brunswick
Shawn R. Craik and Rodger D. Titman

755 Differences in growth of Black Brant goslings between a major breeding colony and outlying breeding aggregations
Christopher A. Nicolai, James S. Sedinger, and Michael L. Wege

767 Diet of the Yellow-knobbed Curassow in the Central Venezuelan Llanos
Carolina Bertsch and Guillermo R. Barreto

778 Landscape configuration effects on distribution and abundance of Whip-poor-wills
Michael D. Wilson and Bryan D. Watts

784 Impact of Hurricane Wilma on migrating birds: the case of the Chimney Swift
Mark Dionne, Céline Maurice, Jean Gauthier, and François Shaffer

793 Red-cockaded Woodpecker home range use and macrohabitat selection in a loblolly-shortleaf pine forest
Douglas R. Wood, Francisco J. Vilella, and L. Wesley Burger Jr.

801 Quality of anthropogenic habitats for Golden-winged Warblers in central Pennsylvania
Jacob E. Kubel and Richard H. Yahner

813 Avian cell-mediated immune response to drought
J. M. Fair and S. J. Whitaker

820 Influence of grazing and available moisture on breeding densities of grassland birds in the central Platte River Valley, Nebraska
Daniel H. Kim, Wesley E. Newton, Gary R. Lingle, and Felipe Chavez-Ramirez

830 Response of songbirds to riparian willow habitat structure in the Greater Yellowstone Ecosystem
Brian F. M. Olechnowski and Diane M. Debinski

840 Regional analysis of riparian bird species response to vegetation and local habitat features
Nadav Nur, Grant Ballard, and Geoffrey R. Geupel

Short Communications

856 First description of the breeding biology and natural history of the Ochre-breasted Brush Finch (*Atlapetes semirufus*) in Venezuela
Luis Biancucci and Thomas E. Martin

862 Reproductive biology of the Red-ruffed Fruitcrow (*Pyroderus scutatus granadensis*)
James A. Muir, Diane Licata, and Thomas E. Martin

867 Nests and nesting behavior of Golden Swallow (*Tachycineta euchrysea*) in abandoned bauxite mines in the Dominican Republic
Jason M. Townsend, Esteban Garrido, and Danilo A. Mejia

871 Nest, nestling care, and breeding season of the Spangled Cotinga (*Cotinga cayana*) in French Guiana
Johan Ingels

874 Nests, eggs, and incubation behavior of the Grey-headed Bullfinch (*Pyrrhula erythaca*)
Jia Chenxi and Sun Yuehua

879 Parental care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) Seedeaters
Carolina Facchinetti, Alejandro G. Di Giacomo, and Juan C. Reboreda

884 Postnatal growth rates of hummingbirds: review and new records
Bernd P. Freymann and Karl-Ludwig Schuchmann

887 Begging behavior of fledgling Rusty-breasted Cuckoo (*Cacomantis sepulcralis*)
Tomáš Grim

891 Natural history of the Red Owl (*Tyto soumagnei*) in dry deciduous tropical forest in Madagascar
Scott G. Cardiff and Steven M. Goodman

897 Bird responses to a managed forested landscape
Richard H. Yahner

901 Freeze-frame fruit selection by birds
Mercedes S. Foster

906 Predation of Rio Grande Wild Turkey nests on the Edwards Plateau, Texas
Justin Z. Dreibelbis, Kyle B. Melton, Ray Aguirre, Bret A. Collier, Jason Hardin, Nova J. Silvy, and Markus J. Peterson

910 No evidence for spring re-introduction of an arbovirus by Cliff Swallows
Valerie A. O'Brien, Amy T. Moore, Kathryn P. Huyvaert, and Charles R. Brown

914 Marbled Godwit collides with aircraft at 3,700 m
Carla J. Dove and Court Goodroe

916 The 2008 William and Nancy Klamm Service Award

917 Ornithological Literature
Compiled by Mary Gustafson and Robert B. Payne

927 Proceedings of the Eight-ninth Annual Meeting

941 Reviewers for Volume 120

943 Index to Volume 120

Contents of Volume 120

THE WILSON JOURNAL OF ORNITHOLOGY

Editor CLAIT E. BRAUN
5572 North Ventana Vista Road
Tucson, AZ 85750-7204
E-mail: TWILSONJO@comcast.net

Editorial Board RICHARD C. BANKS
KATHY G. BEAL
JACK CLINTON EITNIEAR
SARA J. OYLER-McCANCE

Editorial Assistant NANCY J. K. BRAUN

Review Editor MARY GUSTAFSON
Texas Parks and Wildlife Department
2800 South Bentsen Palm Drive
Mission, TX 78572, USA
E-mail: WilsonBookReview@aolcom

GUIDELINES FOR AUTHORS

Please consult the detailed "Guidelines for Authors" found on the Wilson Ornithological Society web site (http://www.wilsonsociety.org). All manuscript submissions and revisions should be sent to Clait E. Braun, Editor, *The Wilson Journal of Ornithology*, 5572 North Ventana Vista Road, Tucson, AZ 85750-7204, USA. *The Wilson Journal of Ornithology* office and fax telephone number are (520) 529-0365. The e-mail address is TWilsonJO@comcast.net.

NOTICE OF CHANGE OF ADDRESS

Notify the Society immediately if your address changes. Send your complete new address to Ornithological Societies of North America, 5400 Bosque Boulevard, Suite 680, Waco, TX 76710.

The permanent mailing address of the Wilson Ornithological Society is: %The Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109. Persons having business with any of the officers may address them at their various addresses given on the inside of the front cover, and all matters pertaining to the journal should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Timothy J. O'Connell, Department of Natural Resource Ecology and Management, Oklahoma State University, 205 Life Sciences West, Stillwater, OK 74078; e-mail: oconnet@okstate.edu

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution. The fund will be administered by the Library Committee. Robert Payne, University of Michigan, is Chairman of the Committee. The Library currently receives over 200 periodicals as gifts and in exchange for *The Wilson Journal of Ornithology*. For information on the Library and our holdings, see the Society's web page at http://www.wilsonsociety.org. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: Josselyn Van Tyne Memorial Library, Museum of Zoology, The University of Michigan, 1109 Geddes Avenue, Ann Arbor, MI 48109-1079, USA. Contributions to the New Book Fund should be sent to the Treasurer.

This issue of *The Wilson Journal of Ornithology* was published on 31 December 2008.

Continued from outside back cover

820 Influence of grazing and available moisture on breeding densities of grassland birds in the central Platte River Valley, Nebraska
Daniel H. Kim, Wesley E. Newton, Gary R. Lingle, and Felipe Chavez-Ramirez

830 Response of songbirds to riparian willow habitat structure in the Greater Yellowstone Ecosystem
Brian F. M. Olechnowski and Diane M. Debinski

840 Regional analysis of riparian bird species response to vegetation and local habitat features
Nadav Nur, Grant Ballard, and Geoffrey R. Geupel

Short Communications

856 First description of the breeding biology and natural history of the Ochre-breasted Brush Finch (*Atlapetes semirufus*) in Venezuela
Luis Biancucci and Thomas E. Martin

862 Reproductive biology of the Red-ruffed Fruitcrow (*Pyroderus scutatus granadensis*)
James A. Muir, Diane Licata, and Thomas E. Martin

867 Nests and nesting behavior of Golden Swallow (*Tachycineta euchrysea*) in abandoned bauxite mines in the Dominican Republic
Jason M. Townsend, Esteban Garrido, and Danilo A. Mejia

871 Nest, nestling care, and breeding season of the Spangled Cotinga (*Cotinga cayana*) in French Guiana
Johan Ingels

874 Nests, eggs, and incubation behavior of the Grey-headed Bullfinch (*Pyrrhula erythaca*)
Jia Chenxi and Sun Yuehua

879 Parental care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) Seedeaters
Carolina Facchinetti, Alejandro G. Di Giacomo, and Juan C. Reboreda

884 Postnatal growth rates of hummingbirds: review and new records
Bernd P. Freymann and Karl-Ludwig Schuchmann

887 Begging behavior of fledgling Rusty-breasted Cuckoo (*Cacomantis sepulcralis*)
Tomáš Grim

891 Natural history of the Red Owl (*Tyto soumagnei*) in dry deciduous tropical forest in Madagascar
Scott G. Cardiff and Steven M. Goodman

897 Bird responses to a managed forested landscape
Richard H. Yahner

901 Freeze-frame fruit selection by birds
Mercedes S. Foster

906 Predation of Rio Grande Wild Turkey nests on the Edwards Plateau, Texas
Justin Z. Dreibelbis, Kyle B. Melton, Ray Aguirre, Bret A. Collier, Jason Hardin, Nova J. Silvy, and Markus J. Peterson

910 No evidence for spring re-introduction of an arbovirus by Cliff Swallows
Valerie A. O'Brien, Amy T. Moore, Kathryn P. Huyvaert, and Charles R. Brown

914 Marbled Godwit collides with aircraft at 3,700 m
Carla J. Dove and Court Goodroe

916 The 2008 William and Nancy Klamm Service Award

917 Ornithological Literature
Compiled by Mary Gustafson and Robert B. Payne

927 Proceedings of the Eighty-ninth Annual Meeting

941 Reviewers for Volume 120

943 Index to Volume 120

Contents of Volume 120

The Wilson Journal of Ornithology

(formerly *The Wilson Bulletin*)

Volume 120, Number 4 CONTENTS December 2008

Major Articles

667 Differential ejection of cowbird eggs and non-mimetic eggs by grassland Passerines
Dwight R. Klippenstine and Spencer G. Sealy

674 Between and within clutch variation of egg size in Greater Rheas
Gustavo J. Fernández and Juan C. Reboreda

683 DNA sequence assessment of phylogenetic relationships among New World martins (Hirundinidae: *Progne*)
Robert G. Moyle, Beth Slikas, Linda A. Whittingham, David W. Winkler, and Frederick H. Sheldon

692 Preliminary analysis of the ecology and geography of the Asian nuthatches (Aves: Sittidae)
Shaily Menon, Zafar-ul Islam, Jorge Soberón, and A. Townsend Peterson

700 Density and abundance of Mountain Plovers in northeastern Montana
Theresa M. Childers and Stephen J. Dinsmore

708 Land cover associations of nesting territories of three sympatric *Buteos* in shortgrass prairie
Scott McConnell, Timothy J. O'Connell, and David M. Leslie Jr.

717 Species recognition in a vocal mimic: repetition pattern not the only cue used by Northern Mockingbirds in discriminating songs of conspecifics and Brown Thrashers
Dustin G. Reichard and J. Jordan Price

725 Lesser Snow Geese and Ross's Geese form mixed flocks during winter but differ in family maintenance and social status
Jón Einar Jónsson and Alan D. Afton

732 Nesting ecology of Common Goldeneyes and Hooded Mergansers in a boreal river system
Hélène Sénéchal, Gilles Gauthier, and Jean-Pierre L. Savard

743 Movements and habitat use by Red-breasted Merganser broods in eastern New Brunswick
Shawn R. Craik and Rodger D. Titman

755 Differences in growth of Black Brant goslings between a major breeding colony and outlying breeding aggregations
Christopher A. Nicolai, James S. Sedinger, and Michael L. Wege

767 Diet of the Yellow-knobbed Curassow in the Central Venezuelan Llanos
Carolina Bertsch and Guillermo R. Barreto

778 Landscape configuration effects on distribution and abundance of Whip-poor-wills
Michael D. Wilson and Bryan D. Watts

784 Impact of Hurricane Wilma on migrating birds: the case of the Chimney Swift
Mark Dionne, Céline Maurice, Jean Gauthier, and François Shaffer

793 Red-cockaded Woodpecker home range use and macrohabitat selection in a loblolly-shortleaf pine forest
Douglas R. Wood, Francisco J. Vilella, and L. Wesley Burger Jr.

801 Quality of anthropogenic habitats for Golden-winged Warblers in central Pennsylvania
Jacob E. Kubel and Richard H. Yahner

813 Avian cell-mediated immune response to drought
J. M. Fair and S. J. Whitaker

Continued on inside back cover

ERNST MAYR LIBRARY
3 2044 114 247 265